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The Comparative Paleoecology of Late Miocene Eurasian Hominoids

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The Comparative Paleoecology of Late Miocene Eurasian Hominoids

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Dedication

This dissertation is dedicated to my grandmother Alma Dinehart Smith who dedicated her working years to science as a scientific illustrator of considerable skill and who has always been an inspiration to her whole family.

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The Comparative Paleoecology of Late Miocene Eurasian Hominoids

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Abstract: Remains of late Miocene hominoids increasingly indicate both taxonomic and adaptive diversity. Understanding hominoid paleoenvironments may illuminate the selection pressures relevant to this diversity. Previous analyses of bovid ecomorphology have been applied to understanding hominoid environments. In this study, a new analysis of distal and complete bovid metapodials assigned to five habitats was conducted and applied to several fossil sites including Can Llobateres and Y0311 in the Siwaliks. An ecomorphological framework was also developed for hipparion metapodials and applied to many late Miocene fossil sites.

The distal and complete discriminant models for bovid metapodials reported here performed between 3.8 and 4.1 times better than chance. Compared to prior discriminant models developed for the bovid femur (Scott et al, 1999; Kappelman, 1988), astragalus (DeGusta and Vrba, 2002) and metapodials (Plummer and Bishop, 1994) all results reported here resulted in more robust values of Press's Q statistic and better performance when compared to chance. Habitat scores were developed for hipparions based mainly on metapodial length and the medial-lateral dimension of the metapodial diaphysis. These

scores yielded paleoenvironmental interpretations congruent with those already published for well-sampled sites such as Höwenegg and provide important evidence regarding late Miocene paleoenvironments.

In total, the results of this analysis indicate two general patterns relevant to late Miocene hominoids. Sites such as Can Llobateres and Rudabánya are marked by lower hipparion diversity, hipparions adapted to closed habitats, and suspensory, frugivorous hominoids. In contrast, a second pattern is evident for locality 12 of the Sinap Formation and Ravin de la Pluie where a diverse and likely abundant hipparion fauna including open-adapted and closed-adapted forms is associated with pronograde, hard object feeding hominoids.

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PART I: INTRODUCTION

Chapter 1: Background and Hypotheses

BACKGROUND

The late Miocene (11-6 Ma) is a time period that is crucial to our understanding the evolution of the human and living ape lineage. Evidence based on genetic differences between living great apes and humans supports the idea that during this time the human lineage diverged from that leading to chimpanzees and gorillas (Sarich & Wilson, 1967; Andrews, 1985; Bailey et al., 1992; Adachi & Hasegawa, 1995; Arnason et al., 1996; Eastseal & Herbert, 1997; Arnason et al., 1998; Stauffer et al., 2001; Nei & Glazko, 2002; Glazko & Nei, 2003; Schrago & Russo, 2003). It is also likely that important hominid adaptations such as bipedalism may first have evolved during this time period (Pickford et al., 2002). Thus, the selection pressures that operated on the late Miocene hominoids were undoubtedly significant influences on the evolution of the Hominoidea.

The late Miocene hominoid record consists mostly of Eurasian representatives descended from Middle Miocene African immigrants. By 13 Ma *Sivapithecus* is known from the Chinji Formation in Pakistan (Kappelman et al., 1991) and by 12 Ma hominoids appear to be well established and diverse across Eurasia (Agusti et al., 1996; Andrews et al., 1996; Andrews & Bernor, 1999). During the Vallesian (Mammal Neogene zones 9 and 10 [ca. 11.2 to 8.7 Ma]) specimens attributed to the hominoid genera *Dryopithecus* (Begun, 1992a; Begun, 1992b; Begun & Kordos, 1993; Moyà-Solà & Köhler, 1995; Andrews et al., 1996; Moyà-Solà & Köhler, 1996; Ribot et al., 1996; Kordos & Begun, 1997; Andrews & Bernor, 1999; Kordos & Begun, 2001), *Ouranopithecus* (de Bonis & Koufos, 1993; Koufos, 1995; de Bonis et al., 1998), *Ankarapithecus* (Alpagut et al.,

1996; Kappelman et al., 1996a; Kappelman et al., 1996b; Begun & Güleç, 1998; Kappelman et al., 2003a; Kappelman et al., 2003b), and *Sivapithecus* (Kelley, 1988; Kappelman et al., 1991; Pilbeam et al., 1991; Cameron et al., 1999; Madar et al., 2002) are relatively well known from sites in Spain, Hungary, Germany, and Austria (*Dryopithecus*), Greece (*Ouranopithecus*), Turkey (*Ankarapithecus*), and India and Pakistan (*Sivapithecus*). By the beginning of the Turolian (ca. 8.7 Ma), this diversity of late Miocene Eurasian hominoids appears to be reduced by extinction. Only the enigmatic, insular endemic *Oreopithecus* is known from the early and medial Turolian of Europe (Andrews et al., 1996; Rook et al., 1996; Moyà-Solà & Köhler, 1997; Rook & Cioppi, 1997; Rook et al., 2000) and only the genus *Sivapithecus* survives in Asia past 9 Ma - disappearing from the fossil record by 8 Ma (Kappelman, pers. comm.). Thus, the Vallesian faunal unit and in particular Mammal Neogene (MN) zone 9 (11.2/10.7 – 9.6 Ma) represents a peak of late Miocene hominoid diversity. The suggestion by some workers (Begun et al., 1997; Stewart & Disotell, 1998) that this diversity of taxa includes the most likely source for an immigrant population to Africa subsequently leading to the African apes and humans makes this time period in Eurasia particularly intriguing from a paleoanthropological perspective.

The Vallesian is also marked by the immigration of hipparionine horses into the Old World at the beginning of MN 9 - ca. 11.2 Ma to 10.7 Ma (Bernor et al., 1988; Kappelman et al., 1996a; Kappelman et al., 1996b; Woodburne et al., 1996; Agusti et al., 1997; Sen, 1997; Agusti et al., 2001; Bernor et al., 2003b; Kappelman et al., 2003a; Scott et al., 2003). This biogeographic event appears to be proceeded closely by the rapid geographic expansion and evolutionary radiation of hipparionines. Hence, a radiation of Vallesian hipparionines appears to co-occur with MN 9 Eurasian hominoids and their extinctions mostly by MN 10 (ca. 9.6 Ma) times. Thus, for a brief window in the late

Miocene, a hipparionine radiation coexisted with biogeographically diverse genera of hominoids. Indeed, only during MN 9 are fossil sites that include both hipparionines and hominoids common. This period of time may represent a window of unique or changing ecological circumstances that is likely to be crucial to our understanding of the evolution of the hominoid lineage. Importantly, the various Vallesian hominoid sites (especially those in Spain, Turkey, and Pakistan) are also part of an increasingly well-defined chronologic framework and therefore offer an opportunity for productive study of the paleoecology of these various hominoids in relation to both chronological (fig. 1.1) and geographical factors (fig 1.2). It is this particular period of hominoid diversity and hipparionine radiation followed by apparent widespread hominoid extinction that is the focus of this thesis.

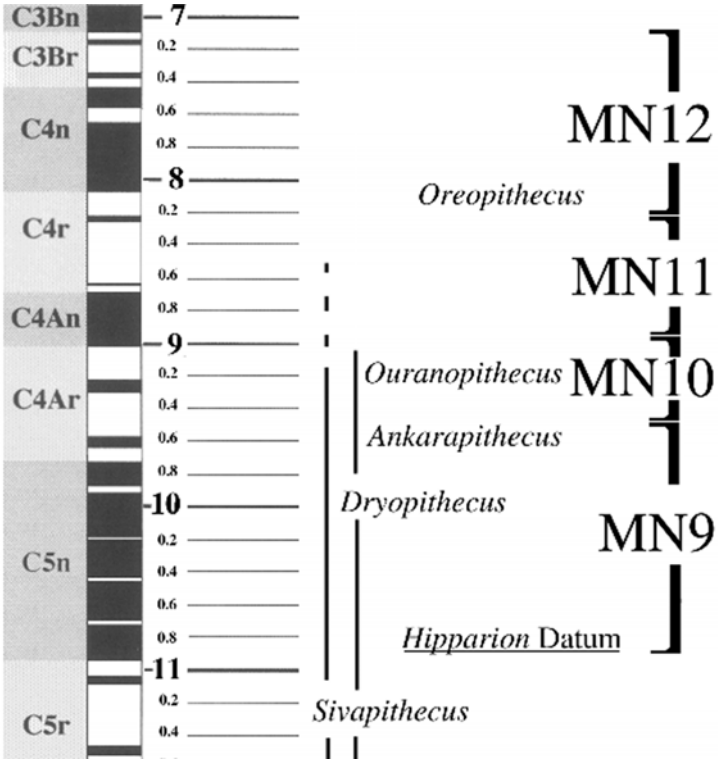


Figure 1.1: Temporal distribution of late Miocene Eurasian hominoids.

GPTS after Cande and Kent (1995).

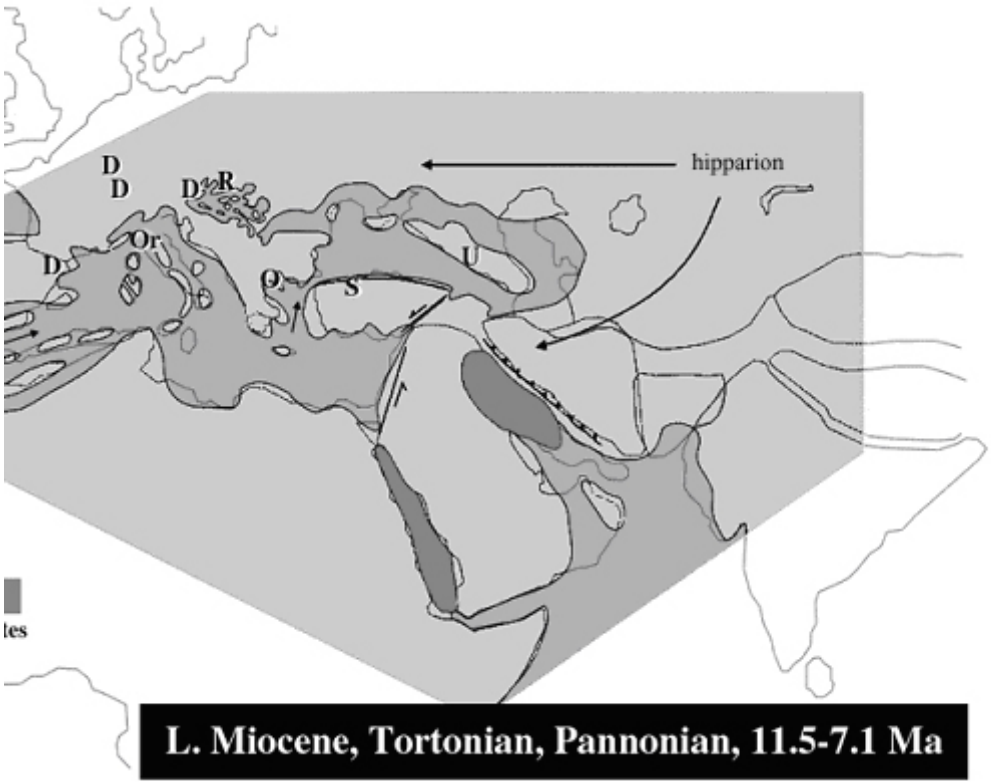


Figure 1.2: Geographic distribution of late Miocene hominoid sites.

D = Dryopithecus sites; R= Rudabánya (Dryopithecus); S = Sinap Formation (Ankarapithecus); Or = Oreopithecus; O = Ouranopithecus; U = Udabno (?Dryopithecus). Map after Rögl (1999).

The late Miocene also appears to have been subject to global changes in climate and possibly regional shifts in ecology. Global changes in vegetation include the presence of C-4 grasses from 15 Ma and their dramatic expansion in the low latitudes between 9 and 4 Ma (Jacobs et al., 1999) or 8 and 6 Ma in at least some areas (Cerling et al., 1997). Some workers (Agusti & Moya-Sola, 1990; Fortelius et al., 1996; Agusti et al., 1997) have proposed a "mid-Vallesian crisis" involving dramatic changes in faunal diversity around 9.6 Ma and perhaps the disappearance of more humid adapted faunal elements. Agusti et al. (2003) suggested a link between hominoid extinction and an increase in

deciduous forest. It is possible that the hipparionine radiation and changes in hominoid diversity are tied to the same underlying ecological and climatic factors.

Two or three late Miocene global cooling events between 12 and 8 million years ago can be discerned in the deep-sea oxygen isotope record (Kennett, 1985; Miller et al., 1991; Kennett, 1995). The two earlier events are dated to before 11 Ma and to between 10.9 Ma and 9.8 Ma while a later more severe event corresponds to between 9.4 and 8.37 Ma (Kennett & Hodell, 1986; see also Scott, 1996). The first of these events would be correlative with MN 9 (ca. 11.2 Ma – 9.5 Ma) while the second spans most of MN 10 (9.6 Ma – ca. 8.7 Ma and most of MN11 (ca. 8.7 Ma – 7.5 Ma) (Bernor et al., 1996a; Kostopoulos et al., 2003). Thus, the first event is correlative with the immigration and radiation of hipparionines in the Old World and possibly earlier hominoid extinctions, while the second event is correlative with the last hominoid extinctions. These general climate-extinction/radiation associations suggest climatic forcing of hominoid extinctions similar to that suggested by turnover-pulse models of evolutionary change (Vrba, 1985). Indeed, it is tempting to link the events characterized as the "mid-Vallesian crisis" and changes in hominoid diversity with extrinsic factors such as climate change. However, the nature of the "mid-Vallesian crisis" is poorly understood and is in need of further study.

The various faunal and climatic changes discussed here may have resulted in significant environmental flux and powerful selection pressures on the late Miocene hominoids. Our understanding of the evolutionary history of this group clearly depends on integrating studies of hominoid morphology with studies of their likely habitats. The adaptations of associated fauna (especially bovids) have been used to make inferences regarding habitats that would have been available to various hominoid taxa (Kappelman, 1988; Kappelman, 1991; Plummer & Bishop, 1994; Spencer, 1995; Kappelman et al.,

1997; Spencer, 1997; Scott et al., 1999). The same approach was used in this study. Specifically, the functional morphology of bovid and equid metapodials was used to make inferences regarding the habitats that would have been available to late Miocene Eurasian hominoids. The metapodials of these two groups are well preserved at both hominoid and non-hominoid sites and present the opportunity for comparative paleoecological studies.

Previous work used a functional model of the bovid femur to achieve paleoenvironmental reconstructions relevant to hominoid evolution (Kappelman, 1988; Kappelman, 1991; Kappelman et al., 1997; Scott et al., 1999). In these studies, hypotheses of function relating to environment were developed and measures were designed to describe relevant morphology. The functional hypotheses were then tested and when the original hypothesis was supported, the morphology in question was used to make paleoenvironmental inferences. In this case, the extensive extant African bovid radiation provided a comparative sample to test the original functional hypotheses. Discriminant function analysis was used to test the functional hypotheses and classify unknown fossil specimens by likely habitat preference. The same techniques were used in this study for those parts dealing with bovids (Chapter 2) while somewhat modified methods mostly developed here (but see also Bernor et al., 2003b; Scott & Maga, in press) were used for study of equid metapodials (Chapters 3-6).

HYPOTHESES

This study aims to explicitly test various alternative hypotheses that fall into two groups. The first group concerns the various hypotheses relating to the functional morphology of fossil bovids and hipparionines. The second group concerns the distribution of environments in the late Miocene as well as the distribution of hominoids with respect to environments.

Specific Functional Hypotheses

The following two hypotheses will serve as the starting points for the analysis of hipparionine metapodials (see primarily Eisenmann, 1995):

1) Relatively elongate third metapodials are adaptive for open country running (and, by extension, open habitats) (Gregory, 1912).

2) Relatively broad (mediolaterally expanded) third metapodials are adaptive in closed or wet habitats (Gromova, 1949; Gromova, 1952).

Similarly, the same two hypotheses will inform study of the bovid canon bones. Functional hypotheses concerning the bovid metapodials are detailed in greater depth in Chapter 2.

Paleoenvironmental Hypotheses

The following four hypotheses will be considered with respect to paleoenvironments in the late Miocene of Eurasia:

1) The distribution of habitat types varies along an east to west gradient.

2) The distribution of habitat types varies with time.

3) The distribution of habitat types varies with global climate.

4) The distribution of habitat types is variable in time and space.

The first hypothesis predicts a greater number of one habitat type to the east or west and is implied by the discussion of Fortelius et al. (1996) of a 'mid-Vallesian crisis.' The second hypothesis would require that reconstructed habitats shift monotonically in one direction with time. The third hypothesis would predict a correlation between habitat type shifts and the global cooling events discussed earlier. The fourth hypothesis implies other possibilities for the patterning of late Miocene habitats. It is important to point out that these hypotheses are not mutually exclusive and can each be evaluated independently.

Hominoids

The five hypotheses listed below are a sampling of hypotheses generated when information regarding the presence/absence of hominoids at sites and what is known of their adaptations can be combined with paleoenvironmental data.

1) Hominoid species with suspensory adaptations are found in habitats with closed canopies while hominoids with generalized quadrupedal adaptations are found in habitats lacking closed canopies.
2) Habitat types track cladistic relationships among hominoid species.
3) Late Miocene hominoid species tend to be found only in habitats with closed canopies.
4) Hominoid species that survive until the latest Miocene are found only in habitats with closed canopies.
5) Well-sampled sites lacking hominoid species represent habitat types not available at hominoid fossil sites and possibly unsuitable for hominoids.

These hypotheses can be evaluated qualitatively as new data emerges on both hominoid and non-hominoid sites. For instance, my analysis of the Sinap hipparionines (in Bernor et al., 2003b)fails to support hypothesis three above (Late Miocene hominoid species tend to be found only in habitats with closed canopies).

SUMMARY OF GOALS AND GENERAL REMARKS

The aim of this study is to provide data relevant to evolutionary forces and selection pressures influencing hominoid evolution. The study of associated fauna from a functional morphological perspective as outlined here provides for the beginnings of a more comprehensive paleoanthropological synthesis by contributing data on hominoid paleoenvironments. This synthesis should ultimately incorporate evidence regarding

hominoid adaptations and systematics with information on paleoenvironments and probable selection pressures.

The ultimate goal of research characterized as "paleoecology" should be to as much as possible approach questions of ecology as studied by neontologists. Thus, paleoecology should ultimately ask questions about organisms, their niches, and their interactions over time. Such a complete synthesis is beyond the scope of any single project but this work is intended as a contribution towards that goal.

With this goal in view, this work is a departure from previous efforts in hominoid and hominid paleoecology in four main ways. Analysis is based on habitat specific adaptations and not on taxonomic indicators. The focus is on specific larger taxonomic groups (bovids and equids) with a general ecological role and not on total species composition of a fauna. The abundance and diversity of different taxa in an assemblage is considered important. And finally, equal scrutiny is applied to fossil sites from which no hominoids are recorded at this time.

Early work in paleoecology (e.g., Andrews et al., 1979) has generally been approached in terms of some kind of ecological diversity analysis. Modern environments were profiled in terms of ecological diversity by diet, body size, locomotor category, or taxonomic group and these profiles were compared to similar profiles for fossil sites. One limitation recognized for this approach is a heavy reliance on taxonomic identifications to provide data on various ecological categories. Various workers have recognized that this program is limited when extinct species differ adaptively from their nearest extant relatives (see particularly Kappelman, 1987; Solounias & Dawson-Saunders, 1988; Kappelman, 1991; Plummer & Bishop, 1994). The proposed solution is a "taxon-free" approach whereby habitat preferences are reconstructed using principles of functional morphology (hence the term ecomorphology). This study departs from the taxonomic

uniformitarianism of earlier work and is in this sense "taxon-free" and is in the tradition of other work described as ecomorphology.

Ecomorphological and theoretically "taxon-free" approaches to paleoecology using ecological diversity methods have been used more recently to reconstruct past environments (e.g., Reed, 1997; Reed, 1998). The relative representation of species in various trophic and locomotor categories is compared for fossil and modern settings. This work departs from such ecological diversity analyses and explicitly focuses on particular taxa (bovids and equids). While the value of ecological diversity analyses is real, limitations include differences in sampling of fossil sites compared to modern reference habitats (e.g., the differential sampling of carnivores, large mammals, and small mammals) and the problem that descriptions of paleoecological settings are limited by the range of available modern analogs. Modern analogs are often restricted to conservation reserves and in many cases are fast disappearing.

Moreover, there is evidence that fundamental environmental variables differed in the past making uniformitarian assumptions about ecological structure uncertain. For example, it appears that prior to 8 Ma the concentration of atmospheric carbon dioxide was greater than it is now (Cerling et al., 1997). Similarly, evidence for past periods of rapid climate change is mounting (Thouveny et al., 1994; Behl & Kennett, 1996; Schulz et al., 1998; Kemp, 2003). The potential for such fundamental variability in basic environmental variables makes projections of modern settings into the past murky. Here, the approach is to focus on taxa that were common and abundant at various late Miocene and explore the implications of their diversity, abundance, and morphological adaptations. In this regard, hipparionines are particularly interesting in that they are recent New World immigrants into the Old World at the time of peak hominoid diversity.

Ecological diversity analyses emphasize the presence of taxa with a given trophic or locomotor adaptation and do not focus on the place of these taxa in an ecological setting. Here, in contrast, the size of populations of taxa with different trophic and locomotor adaptations and with different habitat preferences is considered theoretically important to understanding paleoecological context. The importance of this was recognized by Kappelman (1991) in his study of Fort Ternan. In that case, although the number of complete bovid femora available for analysis was small, they were identifiable to species and corresponded to the two most numerous taxa found at the site. Thus, it is not unreasonable to weigh these two taxa heavily in reconstructions of the Fort Ternan paleoenvironment. Gentry (1970) first noted that cursorial habitat indicators were more common in one of these taxa (*Oioceros*) than the other (*Protragocerus*) and this observation is born out by the contrasting habitat classifications of these two taxa of light cover and heavy cover respectively (Scott et al., 1999). Thus, in the case of Fort Ternan the common status of the two main taxa analyzed provides evidence regarding paleoenvironment on the habitat scale used by these taxa and provides evidence for niche separation with implications about ecological phenomena such as interspecific competition. It is important to note that the 'taxon-free' label for this analysis only means that taxonomic identification is unnecessary to determine morphological adaptation relevant to environment and ecology (Kappelman et al., 1997; DeGusta & Vrba, 2003). On the other hand, placement of specimens in groups sharing common species identification is highly relevant to ecological questions. Theoretically, members of populations of biological species are united by the exploitation of a common niche. Thus, successfully sorted species or population level groups of fossils may ultimately be considered as niche indicators. The successful sorting of ecologically informative elements into species or population groups is considered a critical goal of this work and is

undertaken intensively for hipparionines in particular where larger fossil samples were available. The approach used here is "taxon-free" in one sense but "taxon-intensive" in another.

Finally, paleoecological study is often incidental to specific sites from which hominids or hominoids are found. The result of this is the fairly common phenomenon of publication of companion papers in high impact journals in which one paper describes a new hominid find or species and another describes its geologic and paleoecological setting (e.g., White et al., 1994; Wolde-Gabriel et al., 1994). The comparative study of where hominoids and hominids did and did not live can be somewhat hampered by this. Accordingly, this study focuses on a broad range of sites including those with and without hominoid finds.

In summary, two potential implications of bovid and equid metapodial adaptations analyzed here are put forward as theoretically relevant to understanding hominoid paleoecology. First, a given metapodial morphology present at a fossil site may represent a species with a specific habitat preference and thus indicate that habitat's availability to hominoid taxa at the same site (as proposed by Kappelman, 1991). Second, specific adaptations may correspond to individual species which are distributed differentially in terms of population size, time, and space. The nature of this distribution and not simply the presence of a species may be ecologically significant. An example of such a significant distribution would be the rapid expansion of hipparionine populations followed in time by stabilizing population sizes and taxonomic diversification observed for sites in the Sinap Formation, Turkey (Scott, 1996; Bernor et al., 2003b; Scott et al., 2003) and discussed in greater depth here (see Chapters 6 and 7).

What follows is divided into three Parts. Part II includes Chapter 2 and is focused on bovid metapodial ecomorphology and discusses a framework for interpretation of

bovid metapodial morphology based on extant forms, interprets those fossil bovid metapodials available for study, and finally discusses implications for hominoid paleoecology. Part III includes Chapters 3-6 and is a comprehensive treatment of equid ecomorphology. Chapter 3 is introductory and outlines the general approach and introduces the idea of a morphologically based habitat score. Chapter 4 explains the methodology used in detail. Chapter 5 presents results and discussion for the investigation of living equids. Chapter 6 is concerned with fossil hipparionines. Part IV consists of Chapter 7 and is a discussion of implications for hominoid evolution.

PART II: BOVID ECOMORPHOLOGY

Chapter 2: Habitat Specific Adaptations of Bovid Metapodials and Late Miocene Hominoid Paleoenvironments

INTRODUCTION

Comparisons of eastern and western Eurasian hominoid localities may be of particular significance to our understanding of hominoid evolution (Agusti et al., 1996; Fortelius et al., 1996). To facilitate such a comparison, a functional model is developed here relating bovid habitat preference and bovid metapodial morphology. Some assessment of the validity of this model for understanding late Miocene paleoenvironments can be made using bovid metapodials from the comparatively well-understood locality of Pikermi in Greece. The bovid metapodial model is then applied to late Miocene sites in the Siwalik deposits of northern Pakistan and the Valles-Penedes Basin in Spain and initial east-west comparisons are possible for hominoid sites in these deposits.

Previous study of bovid femora from the *Sivapithecus parvada* site Y0311 in northern Pakistan (Scott et al., 1999) has suggested the presence of diverse but primarily forested habitats at Y0311. Metapodial specimens from Y0311 were available to test these conclusions. Additional bovid metapodials from Vallesian sites in Spain including the *Dryopithecus* site of Can Llobateres (Moyà-Solà & Köhler, 1996) provide a western Eurasian comparison for Y0311 in Pakistan.

The extant radiation of the Bovidae is diverse and includes taxa found in a broad range of habitats from dense forest to wide-open secondary grasslands to steep mountainous terrain. The value of bovids as habitat indicators is well-recognized (Gentry,

1970; Scott, 1979; Vrba, 1980; Greenacre & Vrba, 1984; Kappelman, 1984; Scott, 1985; Kappelman, 1986; Kappelman, 1988; Shipman & Harris, 1988; Solounias & Dawson-Saunders, 1988; Kappelman, 1991; Plummer & Bishop, 1994; Kappelman et al., 1997). As bovids are often common at sites of relevance to hominid and hominoid evolution, they are an important part of hominid and hominoid paleohabitat reconstructions.

Early paleohabitat reconstructions relied on taxonomic identifications based on dental and cranial characters and taxonomy was used as a proxy for paleohabitat (Vrba, 1980; Kappelman, 1984). Thus, the presence of taxonomic groups whose extant representatives tend to be associated with a particular habitat was viewed as evidence for that habitat. This approach is limited by the possibility that fossil representatives of extant taxa may well have used different habitats (see Solounias & Dawson-Saunders, 1988). More recently, habitat preferences have been reconstructed based on functional morphology (e.g., Kappelman, 1988). This taxon-free approach infers paleohabitats based on morphological characters with functional advantages in a specific habitat. For fossil sites, habitat-specific adaptations can fill the role of indicator species in extant settings.

Bovids are among the more abundant taxa at many Neogene sites and thus are of particular utility when reconstructing Neogene paleoenvironments. Previous work on bovids has focused on both locomotor (Kappelman, 1988; Kappelman, 1991; Köhler, 1993; Plummer & Bishop, 1994; Kappelman et al., 1997; Scott et al., 1999; DeGusta & Vrba, 2003) and dietary adaptations (Solounias & Dawson-Saunders, 1988; Spencer, 1995; Fortelius & Solounias, 2000). Based on functional morphological considerations, Kappelman (1988; 1991) developed a discriminant model of the bovid femur for classifying bovids according to first a tripartite division and later (Kappelman et al., 1997; Scott et al., 1999) a four part division of habitats. This study focuses on locomotor

adaptations of metapodials. In particular, it focuses on distal metapodials which are more likely to be preserved than other elements (including the femur) as fossils.

Plummer and Bishop (1994) approached bovid metapodials quantitatively and Köhler (1993) made several functional inferences relevant to habitat based on comparative descriptions of various ruminants. Plummer and Bishop (1994) used a stepwise discriminant analysis of unlogged ratios of 14 metric variables to classify bovid metapodials by habitat using a tripartite habitat classification following Scott (1979; 1985) and Kappelman (1988; 1991). Their comparative sample was restricted to African bovids weighing less than 250 kg in three habitat groups. Plummer and Bishop (1994) correctly classified 84% of complete metacarpals, 89% of complete metatarsals, 68% of distal metacarpals, and 70% of distal metatarsals in the sample.

The functional interpretations of their analyses were left for future study with the suggestion that "joint stabilization, shaft shape, and lever arm length" were related to degree of cursoriality and predator avoidance strategy (Plummer & Bishop, 1994). The tripartite habitat division employed in their analysis reflects the importance of predator avoidance strategy and classifies bovids as open, intermediate, or closed forms (Plummer & Bishop, 1994). Bovids are fit to a habitat gradient along which cursoriality or crypsis dominates predator avoidance strategy. Relative availability of cover is considered the chief habitat correlate of predator avoidance strategy (see Kappelman, 1988; Kappelman, 1991).

Köhler (1993) described distal metapodial morphology from the perspective of a functional model relating the splaying of the phalanges to habitat substrate. Accordingly, plains dwelling forms run on phalanges restricted by "railed" articulations with the metapodials that act to prevent metapodial-phalangeal joint disarticulation. In contrast, forms living in environments characterized by "difficult ground" splay the phalanges to

maintain limb support. The distal metapodials are therefore characterized by less "railed" articulations that permit greater lateral movement. Köhler (1993) defined difficult ground as rocky, inclined, or moist and thus forms living in mountainous, and forested and humid habitats are predicted to contrast with plains dwelling forms. Köhler's (1993) model contrasts with that of Plummer and Bishop (1994) by explicitly referencing a substrate model as opposed to a predator avoidance model when making linkages between metapodial functional morphology and habitat. The habitat classifications employed by Köhler (1993) are substrate oriented and are as follows: A1) wooded and moderately humid, A2) wooded and very humid to semiaquatic, B) open, flat and dry, and C) mountainous habitats.

Relative distal limb segment elongation has long been associated with cursoriality and Scott (1979; 1985) noted the association between limb elongation and open habitats. Consideration of lever mechanics predicts that elongate limbs are capable of producing greater velocities while considerations of energetic efficiency suggest that elongation of distal limb segments and proximal migration of limb center of mass would be likely for cursorial mammals (Hildebrand, 1985). These theoretical grounds may explain elongate metapodials among open habitat, cursorial bovids.

Scott (1979; 1985) also found relatively greater midshaft medial-lateral diameters of metapodials in forest and mountain living bovids. This trend can be explained in terms of the relative significance of transverse and sagittal bending during locomotion. Sagittal bending is likely to be most exaggerated during rapid locomotion over courses with few obstacles (see Kappelman, 1988) in open habitats with dry, hard substrates. Transverse bending and in general more eccentric loading would be expected for locomotion in wet, rocky, and more three-dimensional habitats. Greater medial-lateral shaft diameters are

expected as transverse bending increases (Swartz, 1993) as may be the case in closed, wet or mountainous habitats.

Thus, prior work and biomechanical considerations provide several functional hypotheses relevant to bovid metapodial morphology and habitat preference. To further test these hypotheses and develop a robust discriminant model for classifying fossil specimens by habitat, measurements were selected based on their potential relevance to the various functional considerations discussed above. For example, three measurements of the spacing of the sagittal verticilli of the distal metapodials were developed to quantify the relative splaying of the phalanges. Medial-lateral and anterior-posterior diameters were taken at the proximal and distal quartiles to provide additional description of relative bending moments.

Three explicit functional hypotheses to be tested are (see also fig. 2.1):

1) Open habitat bovids splay the phalanges less than other bovids and have more railed metapodial-phalangeal articulations. Splaying of the phalanges acts to maintain limb support over difficult ground and railed metapodial-phalangeal articulations act to prevent metapodial-phalangeal joint disarticulation during cursorial locomotion in open habitats.

2) Open habitat bovids have relatively elongate metapodials. The elongation of the distal limb segment allows both efficient and rapid locomotion particularly critical for open habitat dwellers with flight dependent predator avoidance strategies.

3) Closed habitat bovids have relatively expanded medial-lateral metapodial diaphyseal dimensions. These expanded medial-lateral dimensions resist greater transverse bending resulting from difficult ground and/or more complex three-dimensional habitats.

With respect to these three hypotheses, it is important to note that the proximal mechanism resulting in each of the above potential habitat-morphology linkages may vary. This variation is important as it may well result in mosaic evolution in which specific aspects of metapodial morphology vary in relation to specific habitat features. For example, Kappelman (1988) argued that femoral morphology varied with predator avoidance strategy which in turn varied primarily due to a habitat cover spectrum. Thus, open habitat cursorial bovids appear to have specific femoral head shapes largely explained in terms of more sagittally directed limb movements. This same argument may be applied to discussion of metapodial length. Elongate metapodials appear to be strongly associated with the cursorial locomotion more likely in open habitats. Similarly, the energetic advantage of less distal limb mass may lead to distally gracile metapodials in cursorial open habitat forms (see Dellanini et al., 2003). For these aspects of metapodial variation, a strong correlation with habitat cover is expected.

Köhler (1993) argued that less railed metapodial-phalangeal articulations may occur as a result of moist ground. Moist ground was in turn correlated with a greater likelihood of forested habitat. However, moist ground may also occur in less forested conditions. Thus, less railed metapodial-phalangeal joints might be expected in open but wet habitats. Similarly, Gromova (1949; 1952) argued that medial-lateral reduction of equid metapodials could reflect dry versus wet habitats and the same may prove to be the case for bovids. In this case, medial-lateral expansion of the metapodial diaphysis might reflect forest conditions but have a more direct causal relationship with substrate moisture level. Moist but open environments could also have medial-lateral metapodial diaphyseal expansion.

Thus, mosaic evolution should be included as a potential expectation with respect to bovid metapodials. An elongate metapodial might be expected for an open country

form tied to seasonally flooded plains. This same form might have distal metapodial features convergent with bovids living in humid forests.

MATERIALS AND METHODS

This study extends comparative study to metapodials of bovids across a broad range of sizes (including those exceeding 250 kg) and extends both the taxonomic range of the comparative sample used as well as the diversity of habitats considered beyond that of previous work (e.g. Plummer & Bishop, 1994; Scott et al., 1999). The four part habitat classification of Kappelman et al. (1997) and Scott et al. (1999) is modified to add an additional rocky or mountainous terrain habitat category comparable to Köhler's (1993) type C and Scott's (1979; 1985) groups 4 and 5 (rolling hills and true mountains). Notable taxonomic additions to the comparative sample used in this analysis include *Pantholops*, *Tragelephas oryx*, the forest living bovine *Anoa depressicornis*, the plains bovine *Bison bison*, the rocky or mountainous terrain form *Oreotragus oreotragus*, several species of the subfamily Caprinae, and *Antilocapra americana* (family Antilocapridae). The addition of antilocaprids to a sample of bovids was made because morphology shared by all open habitat bovids and the open habitat specialist, *Antilocapra americana*, is less likely to be the result of common ancestry than morphology shared only by open habitat bovids.

The total comparative sample includes 330 metacarpals and 328 metatarsals drawn from 73[1] extant bovid species and the recently extinct species, *Myotragus balearicus*. Six antilocaprid metacarpals and 11 antilocaprid metatarsals were added to this sample. Specimens are from the American Museum of Natural History (AMNH), the

[1] Three specimens attributed to *Madoqua* sp. from the YPM were also included in the analysis because body mass at death was known for these specimens. These specimens could belong to *Madoqua kirki*, *Madoqua guentheri*, or possibly a third species of *Madoqua*. These specimens were classified in the heavy cover habitat group like *Madoqua kirki* and *Madoqua guentheri*.

Smithsonian (NMNH), Texas Memorial Museum (TMM), Museum of Comparative Zoology (MCZ), and the Yale Peabody Museum (YPM). The number of individuals measured per species ranged from 1 to 15 for metacarpals and 1 to for 14 for metatarsals. Only specimens with completely fused epiphyses were included in the sample and wild-shot specimens were preferred. The complete extant sample is described in Appendix A.

Twenty-eight measurements were taken on both metacarpals and metatarsals (tab. 2.1; fig. 2.2) using Mitutuyo digital calipers. Ten of these measurements are analogous to nine standard measurements described for the Equidae (Eisenmann et al., 1988). To facilitate the evaluation of metapodial scaling within the Bovidae and the comparison of these trends with metapodial scaling in the Equidae, these analogous measurements were used to generate a common size variable referred to as the Metapodial Global Size Variable (MGSV). The MGSV was generated following Jungers et al. (1995) and Gordon (2002; 2003). For equids, this size variable is simply the geometric mean of nine variables: M3, M4, M5, M6, M10, M11, M12, M13, and M14 of Eisenmann et al. (1988) (see also Bernor et al., 1997)and has been applied elsewhere (Bernor et al., 1999; Bernor & Scott, 2003; Bernor et al., 2003b; Scott & Maga, in press). For bovids, MGSV was also equal to the geometric mean of nine variables. These nine variables include eight variables closely analogous to those of Eisenmann et al. (1988) and the geometric mean of the anterior-posterior dimensions of the medial and lateral verticilli of the distal bovid metapodial which was included as the analog of measurement M12 of Eisenmann et al. (1988) (see tab. 2.2). An additional size variable was generated for distal metapodials, the Distal Metapodial Global Size Variable (DMGSV) using the same procedure and is composed only of the five distal dimensions contributing to the MGSV.

Sex specific species means for MGSV and DMGSV were regressed against published sex specific species means for body mass (see Appendix A). Strong

correlations between these variables and body mass indicate that they may be used as proxy measures for body size and these results are shown in figure 2.3 and table 2.3. A subset of specimens from the YPM collected by Roland G. Bauer in 1965 have associated body weight at time of death and these specimens are plotted in figure 2.3 in conjunction with sex specific species means.

Previous studies have recognized that body size is related to habitat and that morphological indices may also be correlated with body size. Plummer and Bishop (1994) regressed metapodial ratios against femoral length as a body size proxy and reported low R-squared values in general for these regressions (R-squared < 0.306). Based on these low R-squared values, no further transformations were performed on the metapodial ratios and consideration of the influence of body size on habitat group membership appears to have been dropped. However, of the 43 regressions reported by Plummer and Bishop (1994) only 12 were non-significant ($p > 0.05$). It appears that body mass is very often significantly correlated with metapodial morphology and that further consideration of body mass is necessary. Scott et al. (1999) used the alternative procedure of log transforming all ratio variables and including a specific variable as a size proxy (femoral head area). The goal of this procedure was to make the effects of size on subsequent analyses transparent. For example, correlation between proxy size and habitat based discriminant functions should provide some estimate of the relationship between body size and habitat. The comparative data set used here includes species larger than 250 kg and even greater correlations between size and morphology are expected. Therefore, a third method was developed to better isolate the contributions of morphology and size to habitat group membership.

To investigate the relationship between metapodial morphology and habitat independent from size, measurements were transformed to generate shape variables

uncorrelated with size. Each measurement was first divided by the MGSV (for the analyses of complete metapodials) or the DMGSV (for the distal analyses). Three additional ratios based on the distance between lateral and medial verticilli in anterior, inferior, and posterior aspects (posterior : inferior, posterior : anterior, and inferior : anterior) were calculated to estimate the potential splay of the phalanges. All of the resulting ratios were logged and tested for significant correlations with the $\log_{10}$ of MGSV (or DMGSV in the case of the distal analyses). Ratios that showed no significant correlation with MGSV or DMGSV were retained for canonical discriminant analyses. Ratios correlated with MGSV were regressed against MGSV and residuals were retained for canonical discriminant analyses[2]. The result was 31 variables not correlated with size available for canonical discriminant analysis of complete metapodials and 20 variables available for the analysis of distal metapodials (tab. 2.4). The variables for relative functional length and relative maximum length were substantially similar and relative functional length was dropped from further analysis in favor of relative maximum length. The posterior naviculocuboid facet was absent from antilocaprid metatarsals and therefore the medial-lateral posterior naviculocuboid facet measurement (PNML) was dropped from further metatarsal analyses.

Discriminant function analyses were carried out using SAS for both distal and complete data sets. These analyses were used to test whether the size-independent variables discussed above can distinguish between bovids (and antilocaprids) of different habitats.

Seven complete and 19 distal fossil ruminant metapodials were available for study from seven late Miocene sites (Appendix B). Body mass estimates were determined for

[2] Residuals based on regressions of ratios against MGSV (e.g., $\log_{10}$(MLEN/MGSV) versus $\log_{10}$(MGSV)) are identical to residuals based on regressions of logged measurements against MGSV (e.g., $\log_{10}$ (MLEN) versus $\log_{10}$ (MGSV)). This is true because $\log_{10}$(MLEN/MGSV) = $\log_{10}$ (MLEN) - $\log_{10}$ (MGSV).

each fossil specimen based on DMGSV and MGSV using the regressions of sex specific species means already described. The discriminant functions based on the extant sample were used to classify all fossil metapodials by habitat category. Fossil metapodials were available from the following seven sites:

1) Pikermi is from the Pikermi Formation in Greece, preserves no known hominoids, has an inferred age of 8.3 to 8.2 Ma, and has a Turolian mammal correlation of MN11 (Steininger et al., 1996; NOW, n.d.).

2) Ballestar is in the Seu d'Urgell Basin in the Pyrenees of Spain, preserves no known hominoids, and has a Vallesian mammal correlation of MN 9 (Agusti, 1982; Agusti et al., 2001; NOW, n.d.).

3) Can Llobateres is in the Valles-Penedes Basin of Spain, preserves hominoid specimens including postcrania attributed to *Dryopithecus laietanus*, has a Vallesian mammal correlation of MN 9, and has a paleomagnetic chronologic assignment to C4Ar (Moyà-Solà & Köhler, 1996; Agusti et al., 2001; NOW, n.d.).

4) Torrent de Fibulines is in Spain with a Vallesian mammal correlation of MN 10 and preserves no known hominoids (de Bonis et al., 1999; NOW, n.d.).

5) Y0311 (=Y 311 in Scott et al., 1999), the type locality for the hominoid *Sivapithecus parvada*, is in the Nagri Formation in Pakistan and has a date of 10 Ma (C5n.2n) based on paleomagnetic correlation (Kelley, 1988; Kappelman et al., 1996a; Barry et al., 2002).

6) Y0496 (=Y 35 in Scott et al., 1999) is in the Chinji Formation in Pakistan, preserves specimens of the hominoid *Sivapithecus indicus*, and has a paleomagnetic chronologic assignment to C5An.2n (ca. 12.3 Ma) (Kappelman et al., 1991).

7) Y0076 (=Y 76 in Scott et al., 1999) is in the Chinji Formation in Pakistan, preserves specimens of the hominoid *Sivapithecus indicus*, and has a paleomagnetic chronologic assignment to C5r (ca. 11.3 Ma) (Kappelman et al., 1991).

Discriminant function analysis develops classification criteria for cases assigned to classes *a priori* and these functions can be used to classify unknown cases (in this case fossil specimens). Discriminant function analysis is also a dimension reduction technique that can be used to summarize between-class variation, much like principal components analysis summarizes total variation. In this case, discriminant functions were used to classify fossil specimens into habitat groups and to identify the variables responsible for between-class variability. The results of any discriminant function analysis will include some specimens that are classified correctly simply by chance. The number of specimens correctly classified by chance may increase as the number of variables included in the analysis increases. Thus, limiting the number of variables used in a discriminant function analysis is important. In general, the sample size of the smallest group should exceed the number of predictor variables by a factor of 3 to 5 (Hair et al., 1992; Poulsen & French, n.d.) and the total sample size should exceed the number of predictor variables by a factor of 20 (Hair et al., 1992). Based on these guidelines, a maximum limit of 9 predictor variables for discriminant analyses is appropriate for this study.

A stepwise discriminant analysis (SAS: Proc Stepdisc, forward selection) was used to select variables by adding them to the analysis in order of their contribution to the models' discriminatory power as measured by Wilks' lambda. New variables were included in the analysis based on a significant result for an F test ($\alpha = 0.15$) from an analysis of covariance in which previously added variables were covariates and the new variable was the dependent variable. No further variables were added to the analysis

when either a maximum of 9 variables were selected or when no variables were significant for the F test ($\alpha = 0.15$). The stepwise procedure limits the subsequent discriminant analysis to those variables providing the best discrimination between habitat groups and limits the intercorrelation between the variables used in the model. Variables not included in the discriminant model may still be significantly related to habitat and therefore table 2.5 summarizes the results of the stepwise analyses for all possible variables. Results from separate Kruskal-Wallis tests (nonparametric one-way ANOVA) for each variable and habitat are also reported (tab. 2.5).

Linear discriminant analysis is preferred but assumes the homogeneity of the within-group covariance matrices. In contrast, quadratic discriminant functions computed from individual within-group covariance matrices make no assumptions with respect to homogeneity of the within-group covariance matrices. Bartlett's modification of the likelihood ratio test (Morrison, 1976) for the homogeneity of the within-group covariance matrices was used to select the linear or quadratic method of discriminant analysis ($\alpha = .01$).

Figure 2.4 shows the proportion of correctly classified cases versus number of predictor variables for linear and quadratic discriminant function analyses of a randomly generated data set of normally distributed variables assigned to five groups with sample sizes comparable to those of the complete metatarsal data set. The linear method minimizes the number of cases correctly classified as additional random predictor variables are added to the model. In contrast, the quadratic method is very sensitive to the addition of new predictor variables. Thus, even a random data set will result in very high rates of correct classification using the quadratic method when many predictor variables are included.

An alternative measure of discriminatory power involves computing the classification error rate with crossvalidation classification of the input data set. Crossvalidation classifies each observation in the data set using discriminant functions computed from all other observations in the data set; the observation being classified is excluded from the determination of the classifying functions. Previous studies of bovid anatomy and habitat (Kappelman, 1988; Kappelman, 1991; Plummer & Bishop, 1994; Kappelman et al., 1997; Scott et al., 1999) reported only the original correct classification rates (resubstitution accuracy) and did not include the crossvalidated classification summary (crossvalidation accuracy). DeGusta and Vrba (2003) used alternate measures of accuracy where crossvalidation was performed on one specimen for each species as opposed to all of the specimens in the analysis, and where the data set was partitioned into a generator and test subsample. Crossvalidation was preferred here since it does not require estimates of accuracy to be based on discriminant analyses using reduced sample sizes.

The percent of cases classified correctly for the random data set with crossvalidation versus number of predictor variables is also charted in figure 2.4. The number of cases classified correctly with crossvalidation is free of the bias stemming from non-independence of classified observations and discriminant functions. The crossvalidated random data set is not sensitive to the number of predictor variables and the rate of cases correctly classified does not appear to depart from the prior probability of correct classification (where the prior probability is equal to the inverse of the number of groups - 0.20 in this case) (see fig. 2.4). Thus, while crossvalidation may yield lower levels of correct classification, it provides a much more robust measure of the actual utility of discriminant functions. This is especially true as more predictor variables are added to quadratic discriminant analyses.

The likelihood ratio test of the within-group covariance matrices indicated significant differences between the within-group covariance matrices ($p<.001$) for the distal and complete data sets for both metatarsals and metacarpals. Consequently, quadratic discriminant analyses were performed. Both the original classification rates and crossvalidated classification rates are provided as measures of discriminatory power (tab. 2.6). Fossil specimens were assigned to habitat categories using the quadratic discriminant functions based on the total sample of extant specimens.

RESULTS

Summary statistics are given for all metapodial variables for each habitat group (tab.2.7) and for each species (Appendix A).

Metapodial length

Habitat is associated with relative metapodial length. Figure 2.5 plots logged values of MLEN versus MGSV for both metacarpals and metatarsals. The slopes of the significant regression lines in figure 2.5 are both significantly below one and indicate that both metacarpal and metatarsal lengths are negatively allometric (see tab. 2.4). In general, forest and mountain habitat bovids fall below these lines while plains and light cover forms fall mainly above these lines (fig. 2.5). Thus, relative metacarpal and metatarsal lengths as measured by the residuals for $\log_{10}$(MLEN/MGSV) versus $\log_{10}$(MGSV) (= rcMLEN, summarized in tab. 2.7) tend to differentiate specimens from different habitats. Nonparametric Kruskal-Wallis tests comparing rcMLEN across habitat groups are significant ($p<.001$) confirming the association between relative metapodial length and habitat.

The 95% confidence limits for the means of rcMLEN of metatarsals and metacarpals for the forest and mountain habitat specimens each do not overlap with the

95% confidence limits for any other habitat. In contrast, the heavy cover, light cover, and plains groups overlap with each other at the 95% confidence level. Thus, in general as measured by rcMLEN, mountain forms have extremely short metapodials, the forest habitat forms have relatively short metapodials, and plains, light cover and heavy cover forms have relatively long metapodials.

Metapodial diaphyseal shape

Eight measurements (tab. 2.1) were taken on the metapodial diaphyses. Eight size independent diaphyseal shape variables were derived from these measurements and MGSV for both metatarsals and metacarpals. Two size independent variables were derived form DDML and DDAP in conjunction with DMGSV. The logged ratio of PQAP/MGSV (= $\log_{10}$(PQAP/MGSV) = cPQAP) was not significantly correlated with the $\log_{10}$ of the size variable MGSV for either the metatarsal or metacarpal and cPQAP was used as a shape variable describing the relative anterior-posterior expansion of the diaphysis. The metacarpal values for cDQAP and metatarsal values for cPQML and cMAP were also uncorrelated with MGSV. Thus, these variables describe the anterior-posterior expansion of the distal metacarpal diaphysis, the medial-lateral expansion of the proximal metatarsal diaphysis, and anterior-posterior expansion of the metatarsal diaphysis at midshaft respectively. The remaining logged ratios of diaphyseal measurements over size variables were significantly correlated with size and residuals for these measurements were used as shape variables. The shape variables used are summarized by habitat in table 2.7.

All of the shape variables of metapodial diaphyses are significantly associated with habitat ($p<.001$, Kruskal-Wallis test) and indicate four clear morphological trends (fig. 2.1). These are: 1) expanded relative distal anterior-posterior diaphyseal dimensions in closed habitat bovids, 2) reduced relative medial-lateral diaphyseal dimensions in open

habitat bovids, 3) expanded relative medial-lateral diaphyseal dimensions in mountain habitat bovids, and 4) reduced relative anterior-posterior diaphyseal dimensions in mountain habitat bovids.

The variables rcDQAP (metatarsal), cDQAP (metacarpal), and rdDDAP (metatarsal and metacarpal) reflect that closed habitat bovids are distinguished by relatively expanded dimensions of the distal diaphysis in the anterior-posterior direction (tab. 2.7). Metatarsal rcDQAP is high for the forest group, intermediate for light cover and heavy cover (intermediate) habitat groups, and low for the mountain and plains groups. The 95% confidence limits of the rcDQAP mean for the forest habitat metatarsals do not overlap with the 95% confidence limits of the mean for any other habitat group. The intermediate habitat groups overlap at the 95% confidence level, as do the mountain and plains groups. However, neither the mountain nor the plains group overlaps with either of the intermediate habitat groups at the 95% confidence level. Metacarpal cDQAP displays the same trend: the means for cDQAP decline successively from forest to heavy cover to light cover to plains, although the 95% confidence levels do overlap for adjacent habitat groups. The 95% confidence level for the plains group overlaps with the light cover and mountain habitat groups but not with the forest and heavy cover groups. The variables rcDDAP and rdDDAP differ only in the size variable used (rdDDAP uses DMGSV as the size variable to enable the analysis of distal metapodial fragments) and generally reflect the same trend: a distally expanded diaphysis in closed habitat bovids. For metacarpals, both rcDDAP and rdDDAP have means for light and heavy cover that are distinct from each other at the 95% confidence level and means for the forest and plains group distinct at the 95% confidence level. The pattern is clearest for rdDDAP where the forest and heavy cover groups overlap at the 95% confidence level and are high compared to the light cover group, which is high compared to the mountain and

plains groups. For metatarsals, rcDDAP and rdDDAP are high for the forest and intermediate habitat forms compared to the mountain and plains forms; the forest and intermediate forms do not overlap with either the plains or mountain forms at the 95% confidence level.

The general trend is for open habitat forms to have reduced relative medial-lateral diaphyseal dimensions for metacarpals and metatarsals. The variables rcMML, rcPQML (metacarpal) , cPQML (metatarsal), and rcDQML are all reduced for light cover and plains (more open habitat) taxa. For these variables, the plains group has the lowest mean, followed by light cover with the second lowest mean, then heavy cover, and then either the forest or mountain group. In all cases, the mountain group is the only group the forest group ever overlaps with at the 95% confidence level. In particular, the proximal diaphyseal variable of the metatarsal, cPQML, yields means for the forest, heavy cover, light cover, and plains groups that fall along a clear gradient from high to low and do not overlap at the 95% confidence level. The analogous metacarpal variable rcPQML has the same pattern with the exception that the means for the intermediate habitat groups overlap at the 95% confidence level. For both the metacarpal and metatarsal, the plains group has the lowest mean rcMML and overlaps with no other group at the 95% confidence level. In the case of the metatarsal, rcDQML is particularly diagnostic: the means of rcDQML decline from forest to heavy cover to light cover to plains and are distinct from each other at the 95% confidence level. For the metacarpal, the means of rcDQML for the heavy cover and plains groups each overlap the light cover group at the 95% confidence level.

Mountain forms exhibit relatively large values for variables summarizing the relative medial-lateral expansion of the diaphysis. This trend is particularly evident for the distal diaphyseal variables rcDDML and rdDDML in the case of both metatarsals and

metacarpals where the mountain group has the highest mean and does not overlap with any other group at the 95% confidence level. In the case of metacarpals, the means for rcMML and rcDQML are distinct for the mountain group at the 95% confidence level.

Mountain taxa also exhibit a relative reduction of the diaphysis in the anterior-posterior dimension. This reduction can be seen in the variables of the distal diaphysis as already noted. The mountain group also has the lowest means for cMAP (metatarsals), rcMAP (metacarpals) and cPQAP (both metatarsals and metacarpals). These means for the mountain group do not overlap with any other habitat group at the 95% confidence level.

According to the descriptive statistics in table 2.7 and summary in tab. 2.8, the diaphyseal variable that best distinguishes specimens from different habitats appears to be rcMML in the case of metacarpals and either rcDQML or cPQML in the case of metatarsals. These medial-lateral variables describe a morphological gradient of decreasing relative medial-lateral diaphyseal dimensions from closed and mountainous habitat living forms to open habitat forms. This morphological trend can be observed in figure 2.6 where forest and mountain habitat metacarpals generally plot above the regression line of MML versus MGSV and plains habitat metacarpals generally fall below the line (the variable rcMML is equal to the deviation from this line). The trend is similar in figure 2.7 where PQML is plotted versus MGSV.

Distal epiphyses

Three variables of the distal epiphyses were designed specifically to quantify the extent to which phalanges splay in extension (see fig. 2.1). These variables are: INFANT = $\log_{10}$(IVML/AVML), POSANT = $\log_{10}$ (PVML/AVML), and POSINF = $\log_{10}$ (PVML/IVML) (see tab. 2.7). Thus, large values for these variables suggest increasing medial-lateral distances between the verticilli of the metapodials as the verticilli track

from anterior (also dorsal or cranial) to posterior (also caudal or palmar). Metapodials with larger values for INFANT, POSANT, and POSINF should splay the phalanges farther apart as the metapodial-phalangeal joint "screws" into extension. All three variables were regressed against size (in this case the variable DMGSV was used). For both metatarsals and metacarpals, INFANT and POSINF were significantly correlated with size while POSANT was not (tab. 2.4). The residuals for INFANT and POSINF, rINFANT and rPOSINF, were used in subsequent analyses as was the size independent ratio POSANT. Results of nonparametric Kruskal-Wallis tests by habitat group were significant ($p<.001$) for rINFANT and rPOSINF among metatarsals and for POSANT, rPOSINF ($p<.001$), and rINFANT ($p<.05$) among metacarpals.

The variable rPOSINF was high for metapodials from forest and intermediate habitats and reduced for metapodials from plains and mountain habitats. The mean of the plains habitat group did not overlap with the means of the forest and intermediate habitat groups at the 95% confidence level. In metacarpals, POSANT was elevated towards the closed end of the habitat spectrum and reduced towards the open end of the habitat spectrum. In metatarsals, a contrasting trend can be observed for the variable rINFANT: the plains group is distinguished by a larger mean, distinct from the forest and intermediate groups at the 95% confidence level.

Each measurement of the distal epiphysis was used to derive a variable for the distal analysis using the size variable DMGSV as well as a parallel variable for the complete analysis using the size variable MGSV. Thus, each measurement of the distal epiphysis resulted in parallel distal and complete variables (e.g., LVAP resulted in rcLVAP and rdLVAP). The fifteen measurements of the distal epiphysis in conjunction with MGSV and DMGSV resulted in 30 variables of the distal epiphyses for metacarpals and 30 variables of the distal epiphyses for metatarsals. Only one of these variables,

cDEAP for metatarsals, showed no significant result ($p>.05$, Kruskal-Wallis test) in a comparison across all five habitats. In general, the morphological pattern described by a given variable was redundant between metatarsals and metacarpals and not sensitive to the use of DMGSV or MGSV. The apparent relationship between morphology and habitat for each variable is summarized in table 2.8 with respect to three criteria. First, for each variable, any habitat groups that do not overlap at the 95% confidence level of the mean with any other habitat group are noted. Second, the means of the forest and plains groups are compared and significant differences are noted. Third, variables with a monotonic trend in the means from forest to heavy cover to light cover to plains are noted.

In the case of 10 measurements of the distal epiphyses (EMAP, ILAP, AVML, IVML, PVML, ADML, IDML, PDML, DEML, and IIML) of the metacarpals and metatarsals, the mountain habitat could be distinguished at the 95% confidence level from all other habitat groups in both the distal analysis and complete analysis (tab. 2.8). LVAP, MVAP, IVML, and ADML, resulted in variables derived in conjunction with MGSV and DMGSV for both the metacarpals and the metatarsals where the means of the forest group were significantly smaller than the means for the plains group ($p<.05$, Kruskal-Wallis test). The means of the variables rcMVAP, rcIMAP, rcIVML and rcADML (derived using MGSV) increased monotonically across the closed to open habitat spectrum in both metacarpals and metatarsals. For metatarsals only, rcIDML displayed a similar monotonic trend. The variables rcELAP, rcEMAP, and rcILAP all increased monotonically across the closed to open habitat spectrum in metacarpals only.

Proximal epiphyses

The variables cPML and cPAP were significantly correlated ($p<.05$) with size as measured by MGSV in the case of metacarpals, and the residuals rcPML and rcPAP were

summarized. No major trends with respect to habitat were evident for these variables (tab. 2.8).

In the case of metatarsals, cPAP was significantly correlated with MGSV whiles cPML was not. Thus, cPML and the residual rcPAP were summarized. The means for the forest and plains groups were significantly different for rcPAP and cPML of the metatarsals. The forest group displayed elevated values for cPML and reduced values for rcPAP compared to the plains group. The trends for rcPAP and cPML were monotonic across the closed to open habitat spectrum; the mean for rcPAP increased from forest to heavy cover to light cover to plains and cPML decreased from forest to heavy cover to light cover to plains.

The measurement PNML was unavailable for antilocaprids and was not used in later discriminant analyses (as already noted under Methods). However, the variable rcPNML was significantly elevated for forest bovids compared to plains bovids. Similarly, cMGML was elevated for the forest group compared to the plains group (tab. 2.8).

Discriminant function analysis of extant bovids

Stepwise selection of variables

The results of stepwise discriminant analyses used in the selection of variables for four separate canonical discriminant analyses are shown in table 2.5. Variables are ranked by Wilks' lambda in table 2.5 and for each analysis (complete metacarpal, distal metacarpal, complete metatarsal, and distal metatarsal) the nine variables with the greatest Wilks' lambda were used. In the case of each analysis, more variables were available for addition to the analysis based on the F test ($\alpha = 0.15$) from an analysis of covariance in which previously added variables were covariates and new variable was the

dependent variable. However, the addition of more variables would have raised the number of predictor variables above the limit of nine set by considerations of sample size.

Complete metatarsal

Discriminant function analysis of the complete metatarsal was based on five variables of the diaphysis (rcMML, rcDDML, rcDDAP, cPQML, cPQAP), three variables of the distal epiphysis (rcIDML, rcLVAP, and rcILAP), and one variable describing relative length (rcMLEN). Of these variables, rcMML had the highest Wilks' lambda and supplied the most discriminatory power to the discriminant model (tab. 2.5). The analysis generated four canonical variables with significant canonical correlations ($p<.05$). The first two canonical variables accounted for 91.3% of the variance (tab. 2.6). The complete metatarsal quadratic discriminant model correctly classified 277 (81.7%) of extant specimens. The number of specimens classified correctly was 239 (70.5%) when calculated with crossvalidation. With crossvalidation, correct classification was lowest for the light cover group (56.2%) followed by heavy cover (64.1%), plains (75.5%), mountain (82.5%), and the plains groups (84.6%) (tab. 2.6). Thus, the discriminant model was least effective at distinguishing the two intermediate habitat types. However, collectively specimens from the two intermediate habitat groups were either assigned correctly to their own habitat group or to the other intermediate group at a rate of 83.0% with crossvalidation. This rate is comparable to the rates of correct classifications for the forest and plains groups.

Since the first two canonical variables explained most of the variance in the discriminant model, the relationships between the morphological variables and canonical variables can be shown in two dimensions. Figure 2.8A plots the total canonical structure for the first two canonical variables. The correlations for each morphological variable

with the first two canonical variables are plotted and a vector drawn representing the relationship between each morphological variable and the two-dimensional canonical variable space capturing the majority of habitat related variability. The complete canonical structure for the analysis of the complete metatarsal is reported in table 2.9.

A strong negative correlation is evident between canonical variable one (CV1) and rcMLEN, while rcMML and cPQML have strong positive correlations with CV1. CV1 tends to separate specimens along a habitat spectrum from open habitats to closed habitats (fig. 2.9A). Plains habitat specimens have the most negative scores on CV1 indicating reduced measures for rcMML and increased measures for rcMLEN. Forest habitat specimens have positive scores for CV1 and have corresponding low values for rcMLEN and rMVAP and high values for rcMML.

CV2 mainly separates the mountain habitat group from all others. The mountain group has positive scores for CV2 compared to all other groups. CV2 has strong positive correlations with rcDDML and rcIDML. Thus, mountain habitat forms have expanded medial-lateral measurements distally. CV2 has strong negative correlations with the anterior-posterior variables cPQAP, rcDDAP, and rcILAP indicating a reduction in the anterior-posterior metapodial dimensions of mountain habitat bovids. A negative correlation between CV2 and rcMLEN indicates that, like forest living bovids, mountain habitat forms have relatively short metapodials.

Complete metacarpal

The nine variables selected for discriminant analysis included the diaphyseal variables (rcMML, rcDDAP, and rcDDML), the relative length variable (rcMLEN), and the distal epiphyseal variables (rcAVML, rcLVAP, rcEMAP, rcADML, and rcDEML). These results are substantially analogous to those for the complete metatarsal. The only differences between the two analyses in terms of variables included were the inclusion of

rcAVML, rcADML, rcEMAP, and rcDEML and exclusion of cPQAP, cPQML, rcIDML, and rcILAP in the complete metacarpal analysis. It is worth noting that rcADML and rcIDML are both medial-lateral measures of the distal articular surface and quite possibly reflect similar constraints. Similarly, rcILAP and rcEMAP are both anterior-posterior measures of the distal articular surface. Thus, the major difference between the complete metatarsal and complete metacarpal analysis appears to be the inclusion of rcAVML and rcDEML and exclusion of cPQAP and cPQML in the complete metacarpal analysis.

As was the case with the complete metatarsal analysis, the most discriminatory power in the discriminant model was supplied by rcMML which had the highest Wilks' lambda (tab. 2.5). The complete metacarpal analysis generated four significant canonical correlations ($p<.05$) and the first two accounted for 89.7% of the variance (tab. 2.9). The discriminant model generated quadratic functions which correctly classified 261 of 336 extant specimens (77.7%) (tab. 2.6). With crossvalidation, this overall figure drops to 227 (67.6%) correctly classified specimens. With crossvalidation, correct classification was lowest for the heavy cover group (54.7%) followed by light cover (59.3 %), forest (71.7%), plains (77.3%), and the mountain group (80%). When light cover and heavy cover are combined, 72.9% of specimens are classified as either light or heavy cover using crossvalidation. Compared to the complete metatarsal model, the overall summary of correct classification appears slightly less robust for complete metacarpals. Most of the reduction in the power of the complete metacarpal model comes in the forest group where only and 71.7% of specimens were correctly classified with crossvalidation as opposed to 84.6% in the complete metatarsal analysis.

As with the complete metatarsal model, the first two canonical variables explained most of the variance and the relationships between the morphological variables and canonical variables can be shown in two dimensions. Figure 2.8B is based on the

total canonical structure (correlations between variables and canonical variables) and shows vectors diagramming the relationship between each morphological variable and the two-dimensional canonical variable space capturing the majority of habitat related variability. The complete canonical structure for the analysis of the complete metatarsal is reported in table 2.9.

In the complete metatarsal analysis, CV1 was associated primarily with an open to closed habitat spectrum while CV2 appeared mainly to distinguish the mountain group. The results of the complete metacarpal analysis differ: CV1 and CV2 are each associated with both the habitat cover spectrum and mountain group identity. Forest forms have positive scores for CV1 (mean of 0.84) and negative scores for CV2 (mean of -1.75) while plains forms have negative scores for CV1 (mean of -1.37) and positive scores for CV2 (mean of 1.11). The mountain group had strongly positive scores for both CV1 and CV2 (see fig. 2.9B).

CV1 was most strongly correlated with rcMML (positive correlation) and rcMLEN (negative correlation). Other strong correlates of CV1 were rcEMAP, rcMVAP (negative correlation), and rcDDML (positive correlation). CV2 had strongly positive correlations with rcIVML, rcIIML, rcADML, and rcDDML and strongly negative correlations with rcEMAP and rcDDAP.

The negative correlations between CV1 and rcMLEN and rcMVAP and positive correlation between CV1 and rcMML appear to drive a pattern of negative scores on CV1 for more open habitat forms compared to more closed habitat forms. These results are closely analogous to the results for the complete metatarsal analysis. However, open versus closed habitat identity is also captured by CV2.

Mountain forms are clearly distinguished by their positive scores on both CV1 and CV2. The variables rcEMAP and rcDDML appear to describe a morphological trend

that distinguishes mountain forms from all others. rcEMAP has large negative correlations with both CV1 and CV2 and rcDDML has large positive correlations with both CV1 and CV2. Thus, mountain habitat specimens appear associated with small values for rcEMAP and large values for rcDDML.

An important difference between the complete metacarpal and complete metatarsal analysis is in the relationship between the first two canonical variables and habitat variability along two hypothetical axes, one expressing habitat cover and another expressing the frequency of mountainous, steep, or hilly habitats. In the case of the complete metatarsal, visual inspection of figure 2.9A reveals that CV1 corresponds closely to a habitat cover dimension and CV2 corresponds very closely with a nearly orthogonal mountain habitat dimension. The means for the plains, light cover, heavy cover, and forest habitats closely fit a line rotated just less than 19 degrees from the CV1 axis. This close correspondence between CV1 and CV2 and specific habitat components allows the correlations of CV1 and CV2 with morphological variables to be readily interpreted as correlations between these habitat components and morphology. In contrast, the analysis of the complete metacarpal resulted in a CV1 and a CV2 that correspond less closely to habitat cover and the frequency of mountainous, steep, or hilly habitats.

For the complete metacarpal analysis, the trendline based on CV1 and CV2 for the four habitat groups defined by cover is rotated approximately 52 degrees from CV1 and the mountain group mean is rotated about 56 degrees from CV2. Thus, to interpret the correlations between the first two canonical variables and the morphological variables in the same way as in the complete metatarsal analysis it is necessary to rotate figure 2.9B 52 degrees for CV1 to express a habitat cover dimension and 56 degrees for CV2 to express a mountain habitat dimension. The correlations between morphological variables

of the complete metacarpal and the rotated values for CV1 (rotated about 52 degrees) and CV2 (rotated about 56 degrees) are shown in table 2.9.

The correlations between the rotated scores for CV1 and morphological variables indicate that rcMML and rcDDAP are positively correlated with increasingly closed habitats and that rcMLEN and rcLVAP are positively correlated with more open habitats (tab. 2.9). The rotated scores for CV2 are strongly correlated with all the variables in the analysis except rcDDAP and rcLVAP. The three strongest correlates of mountainous habitats are: rcDDML (positive), rcEMAP (negative), and rcAVML (positive) (tab. 2.9).

The relationships between habitat and metacarpal morphology can be summarized as follows. Forest and mountain habitat forms share relatively short metacarpals (indicated by rcMLEN) with relatively expanded diaphyses at midshaft (indicated by rcMML). Plains habitat forms have well-developed verticilli (indicated by rcLVAP) and elongate metacarpals (indicated by rcMLEN). Forest forms also appear to be distinguished by anterior-posteriorly expanded distal metacarpal diaphyses (indicated by rcDDAP). Mountain forms appear to have medial-lateral expansion and anterior-posterior reduction of the distal metacarpal (as indicated by rcDDML and rcEMAP).

Distal metatarsal

Discriminant function analysis of the distal metatarsal was based on nine variables: rdEMAP, rdDDAP, rdMVAP, rdIDML, rdILAP, rdELAP, rdADML, rdPDML, and rdIIML. Of these variables, rdEMAP had the highest Wilks' lambda and supplied the most discriminatory power to the discriminant model. The analysis generated three canonical variables with significant canonical correlations ($p<.05$) and the first two of these explained 91.5% of the variance. The distal metatarsal quadratic discriminant model correctly classified 264 of 340 (77.6%) of extant specimens. The number of specimens classified correctly was 225 (66.2%) when calculated with crossvalidation.

With crossvalidation, correct classification was lowest for the heavy cover group (50.0%) followed by light cover (54.4%), plains (73.4.2%), forest (78.8%), and the mountain group (85.0%) (tab. 2.9). Thus, as in the complete analysis, the discriminant model was least effective at distinguishing the two intermediate habitat types. Collectively, the intermediate habitat specimens were classified in one of the intermediate groups in 71.4% of the cases, which is comparable to the correct classification rates for the plains group.

CV1 and CV2 each distinguished habitat groups along: 1) a habitat cover spectrum and, 2) according to use of mountainous habitats (fig. 2.9C). As in the case of the complete metacarpal, rotation of figure 2.9C was necessary to interpret the correlations between the habitat cover and mountain habitat dimensions and morphological variables. The trend in CV1 and CV2 for the four habitat groups based on cover was rotated approximately 39 degrees relative to the axis for CV1. The centroid for mountain habitats was not orthogonal to this trend and was rotated about 50 degrees relative to the axis for CV2. These correlations and the original unrotated correlations for CV1 and CV2 are shown in table 2.9.

The correlations of the rotated scores for CV1 with morphological variables indicate that rdDDAP and rdMVAP are strong correlates of habitat cover. Forest forms have positive scores for CV1 (rotated and unrotated) and a positive correlation with rdDDAP indicates that forest forms have an anterior-posterior expansion of the distal metatarsal diaphysis. Plains forms have negative scores for CV1 (rotated and unrotated) and a negative correlation with rdMVAP indicates that more open habitat forms have an anterior-posterior expansion of the verticilli of the metatarsal. These results mirror those for the complete metatarsal.

The rotated scores for CV2 have strong correlations with all the variables in the distal metatarsal analysis except rdMVAP. The variable rdEMAP had the highest

correlation with the rotated scores for CV2. Mountain habitat specimens had negative scores for CV2 (rotated and unrotated) and the positive correlation with rdEMAP indicates a relatively reduced anterior-posterior dimension for the distal articular portion of the metatarsal. The complete metatarsal analysis did not include a variable based on EMAP but the similar variable rcILAP was included and suggested a similar anterior-posterior reduction of the distal articular portion of the metatarsal.

Distal metacarpal

Discriminant function analysis of the distal metatarsal was based on nine variables: rdEMAP, rdDDAP, rdMVAP, rdADML, rdDDML, rdDEML, rdIVML, rdIIML, and rdLVAP. Like the distal metatarsal analysis, rdEMAP had the highest Wilks' lambda. Out of three significant canonical variables ($p<.05$), the first two accounted for 92.0% of the variance. The quadratic discriminant model correctly classified 256 of 336 (76.2%) extant specimens without crossvalidation and 210 (63.5%) extant specimens with crossvalidation. With crossvalidation, correct classification was lowest for the light cover group (36.3%) followed by heavy cover (54.7%), forest (69.8%), plains (80.7%), and the mountain group (85.0%) (tab. 2.9). Once again, the discriminant model was least effective at distinguishing the two intermediate habitat types. The performance of the distal metacarpal was particularly poor although it still performed 1.8 times better than chance with crossvalidation. This level of accuracy is still higher than the 1.65 times better than chance without crossvalidation reported previously for distal metacarpals of intermediate habitat bovids (Plummer & Bishop, 1994). Collectively, the intermediate habitat specimens were classified in one of the intermediate groups in 64.5% of the cases which is close to the correct classification rate for the forest group.

As in previous analyses, CV1 and CV2 distinguished habitat groups along both a habitat cover spectrum and according to use of mountainous habitats (fig. 2.9D). In contrast with the other three analyses, CV2 aligns most closely with the habitat cover trend while CV1 distinguishes mountain habitat specimens. This alignment is close enough that CV2 could be interpreted partly as a habitat cover axis while CV1 could be interpreted partly as a mountain habitat axis. However, to allow interpretations comparable to the other analyses, rotations were performed to align CV1 with the habitat cover spectrum and CV2 with a mountain habitat axis. The trend in CV1 and CV2 for the four habitat groups based on cover was rotated approximately 61 degrees relative to the axis for CV1. The centroid for mountain habitats was nearly orthogonal to this trend and was rotated about 64 degrees relative to the axis for CV2. These correlations and the original unrotated correlations for CV1 and CV2 are shown in table 2.9.

The correlations of the rotated scores for CV1 (tab. 2.9) with morphological variables indicate that rdDDAP is the major correlate of habitat cover for the distal metacarpal. Forest forms have negative scores for the rotated CV1 and a negative correlation with rdDDAP indicates that forest forms have an anterior-posterior expansion of the distal metacarpal diaphysis. This result was also observed for the analysis of the distal metatarsal.

The rotated scores for CV2 have strong correlations with all the variables in the distal metacarpal analysis except rdMVAP, rdLVAP, and rdDDAP (tab. 2.9). The variable rdEMAP had the highest correlation with the rotated scores for CV2 and rdDDML had the second highest correlation. Mountain habitat specimens had negative scores for CV2 (rotated) and the positive correlation with rdEMAP indicated a relatively reduced anterior-posterior dimension for the distal articular portion of the metatarsal. The negative correlation between rdDDML and CV2 (rotated) indicated relative distal

expansion of the diaphysis in mountain habitat forms. These results are consistent with those of the other analyses.

Analysis of fossil bovids

The results of the discriminant analysis of extant specimens suggest that metapodial morphology can be used to distinguish bovids of different habitats. The quadratic discriminant functions were applied to complete and distal metapodials from Pikermi (Greece), Ballestar (Spain), Can Llobateres (Spain), Y0311 (Pakistan), Y0496 (Pakistan), and Y0076 (Pakistan). The probabilities of a specimen belonging to each of the five habitat categories are reported for each specimen in table 2.10. The probabilities associated with the most likely habitat category for fossil specimens ranged from 0.309 to 0.999 for distal metapodials and 0.564 to 0.988 for complete metapodials.

The range of probabilities for the most likely habitat category suggested careful consideration of the model results. A meta-analysis was conducted to isolate the importance of individual morphological variables in the determination of a given fossil specimens most likely habitat. Alternative discriminant function analyses were performed starting with the two morphological variables with the highest Wilk's lambda and sequentially adding morphological variables in decreasing order of Wilk's lambda until all nine variables were included. The probabilities of each fossil specimen belonging to each of the five habitat groups were recorded for each step. The most likely habitat assignment is shown for each step for every specimen in table 2.10.

Pikermi

Two metatarsals, YPM VP20693 and YPM VP20692, were available for analysis from Pikermi. YPM VP20693 is a complete metatarsal and YPM VP20692 is a distal

metatarsal. These specimens appear to represent two different species on the basis of body size. Estimates for body mass were determined based on MGSV and DMGSV for YPM VP20693 and based on DMGSV for YPM VP20692 (see Appendix B). YPM VP20693 is estimated to come from an individual weighing 26.2 ×/÷1.48 kg based on MGSV and 22.7 ×/÷1.49 kg based on DMGSV while YPM VP20692 appears to have represented an individual weighing about 161.4 ×/÷1.49 kg (based on DMGSV). The large difference in body mass estimates clearly indicates that the two specimens represent different species.

YPM VP20693 was assigned to the heavy cover habitat category with a probability of 0.841 in the complete metatarsal analysis and to the forest habitat group with a probability of 0.999 in the distal metatarsal analysis. Figure 2.9 and table 2.10 indicate that YPM VP20693 was consistently assigned to the heavy cover category following the addition of the variable rcMLEN. Prior to this YPM VP20693 was assigned to the forest category on the basis of values for rcMML, rcIDML, and rcLVAP. Thus, YPM VP206093 appears be relatively longer than metatarsals of forest bovids but to have a distal morphology consistent with forest bovids.

The larger specimen, YPM VP20692, was assigned to the heavy cover habitat group with a probability of 0.638 and to the light cover group with a probability of 0.135 in the distal metatarsal analysis. On the basis of the first three variables added to the analysis (rdDDAP, rdEMAP, and rdMVAP), YPM VP20692 was classified in the forest habitat group (tab. 2.10). Thus, more closed habitats appear likely for YPM VP20692.

Ballestar

A single complete metacarpal, IPS BA 20617, was available for analysis from Ballestar. Body mass was estimated at 68.6 ×/÷1.68 kg based on MGSV and 64.8 ×/÷1.73 kg based on DMGSV. IPS BA 20617 was classified in the heavy cover group with a

probability of 0.564 and in the light cover group with a probability or 0.436 in the complete analysis. In the distal analysis, IPS BA 20617 was classified in the light cover group with a probability of 0.967. Some type of intermediate habitat would appear most likely for IPS BA 20617.

Can Llobateres

Two complete ruminant metacarpals were available for analysis from Can Llobateres. IPS 2548 has been attributed to a cervid of the genus *Amphiprox* and IPS CLL 20603 to the boselaphine bovid *Miotragocerus pannoniae* (Köhler, 1993). Both specimens were slightly damaged and the measurements LVAP and MVAP were unavailable for IPS CLL 20603 and MVAP was unavailable for IPS 2548. As a result values for MVAP were estimated for both specimens and LVAP was estimated for IPS CLL 20603. Of all measured metacarpal variables, the Pearson correlations with MVAP were greatest with ILAP, IMAP, and LVAP ($r > 0.99$). Similarly, the Pearson correlations with LVAP were greatest with ILAP, IMAP, and MVAP ($r > 0.99$). Therefore, estimates were based on least squares regressions involving these variables. In the case of IPS 2548, MVAP was estimated based on LVAP. For IPS CLL 20603, MVAP was estimated based on IMAP and LVAP was based on ILAP.

Body mass for IPS CLL 20603 was estimated at 111 ×/÷1.68 kg based on MGSV or 102.2 ×/÷1.73 kg based on DMGSV. The cervid, IPS 2548, resulted in body mass estimates using bovid regressions of 28.7 ×/÷168 kg based on MGSV and 25.3 ×/÷1.74 kg based on DMGSV (Appendix B). These body mass estimates are made more uncertain by the fact that DMGSV and MGSV are determined in part by the estimated values for MVAP and LVAP.

IPS CLL 20603 was classified in the light cover category in the complete metacarpal analyses and in the heavy cover category in the distal analysis. The

probabilities associated with these classifications were 0.717 and 0.739 respectively. The second most likely habitat for IPS CLL 20603 was heavy cover in the complete analysis and forest in the distal analysis (Appendix B).

The fact that MVAP and LVAP were estimated for IPS CLL 20603 adds greater uncertainty to its habitat classification. Figure 2.10 shows how the probability of IPS CLL 20603's habitat classification varies with different estimates (expressed in terms of ± standard errors) for MGSV and LVAP in the complete analysis. Raising or lowering the estimate for LVAP by much increases the probability of a heavy cover classification (fig. 2.10A). Raising the estimate for MGSV increases the probability of a heavy cover classification while lowering the estimate of MGSV increases the probability of a light cover classification (fig. 2.10B). No reasonable error in the estimates of MVAP and LVAP (and hence MGSV) led to the classification of IPS CLL 20603 in either the forest, mountain or plains habitat. Some form of intermediate habitat seems most likely for IPS CLL 20603.

IPS 2548, attributed to the cervid *Amphiprox*, was classified in the heavy cover category with a probability of 0.816 in the complete metacarpal analysis and was classified in the forest habitat with a probability of 0.516 in the distal metacarpal analysis. Based on a bovid-antilocaprid comparative sample the fossil cervid *Amphiprox* would appear be either a forest adapted form or an intermediate habitat form. This extrapolation needs to be treated with caution considering the likely taxonomic identity of IPS 2548

Torrent de Fibulines

A single very well-preserved complete metacarpal, IPS 1237, was available from the Spanish MN 10 locality Torrent de Fibulines. IPS 1237 represents a larger bovid with an estimated body mass of about 195.2 ×/÷1.68 kg based on MGSV (196.8 ×/÷1.74 kg

based on DMGSV) and was classified in the heavy cover habitat category with a probability of 0.899 in the distal analysis and 0.988 in the complete analysis.

Y0496

Two distal metacarpals and two distal metatarsals from Y0496 (= Y 35) were classified by the distal discriminant analyses. All specimens had probabilities associated with the most likely habitat classification greater than 0.860. Two specimens were classified in the light cover group, one specimen was classified in the heavy cover group, and the fourth specimen was placed in the mountain group (tab. 2.10; Appendix B). Body mass estimates based on DMGSV ranged from 16.1 kg to 40.5 kg (Appendix B).

The distal metatarsal, GSP 45529, was classified in the heavy cover habitat group and had an estimated body mass of 16.1 ×/÷1.49 kg. The other three specimens had body mass estimates ranging from 33.2 ×/÷1.49 kg to 40.5 ×/÷1.73 kg.

Y0076

Two distal metapodials from the Chinji Formation locality Y0076 were available for discriminant analysis. Both specimens were classified in the forest group. The probabilities associated with these classifications were 0.919 for the distal metatarsal, GSP 32407, and 0.999 for the distal metacarpal, GSP 46146. Estimated body masses for these specimens based on DMGSV were 31.1 ×/÷1.49 kg and 31.6 ×/÷1.74 kg respectively.

Y0311

A total sample of 14 metapodials was available from Y0311. Of these specimens, 10 were metacarpals and 4 were metatarsals. Most of these specimens were incomplete and only one metacarpal and one metatarsal could be included the complete analysis.

Thus, the distal metacarpal analysis which included 10 specimens represents the largest sample for Y0311.

The sample of 10 distal metacarpals resulted in four specimens grouped in the heavy cover habitat category, three specimens grouped in the forest habitat category, and three specimens grouped in the light cover category (tab. 2.10). The probabilities associated with these classifications ranged from 0.492 to 0.958. GSP 10569 was classified in the forest category with a probability of 0.492, but had a second most likely classification of heavy cover with a probability of 0.486. The more closed end of the habitat spectrum seems likely for GSP 10569. The complete metacarpal, GSP 46729, was classified in the heavy cover habitat category in the distal analysis with a probability of 0.828 and in the heavy cover category in the complete analysis with a probability of 0.872.

The metacarpals from Y0311 appear to fall into two distinct size ranges. Three had estimated body masses ranging from 101.3 ×/÷1.73 kg to 142.1 ×/÷1.74 kg based on DMGSV. The other seven had body masses that ranged from 50.6 to 64.4 (×/÷1.73) kg. Of the larger specimens, two were classified in the heavy cover group and one was classified in light cover group. The seven smaller specimens included three specimens in the forest group, two in the heavy cover group, and two in the light cover group.

Three of the four metatarsals from Y0311 were classified in the light cover habitat group according to the distal analysis. The single complete metatarsal, GSP 46737, was classified in the light cover group in the distal analysis with a probability of 0.758 and in the heavy cover group in the complete analysis with a probability of 0.730. The fourth distal metatarsal from Y0311, GSP 47810, was classified in the mountain habitat group with a probability of 0.309 and had a second most likely habitat of light cover.

The metatarsals could be assigned to the same two general size groupings as the metacarpals. GSP 47810 had an estimated body mass of 116.1 ×/÷1.49 kg based on DMGSV while the other three had body masses ranging from 49.8 kg to 64.4 (×/÷1.49) kg based on DMGSV (Appendix B).

DISCUSSION

Reclassification of Extant Bovids

Prior studies (Kappelman, 1991; Plummer & Bishop, 1994) have reported taxa in which more than one half of the specimens are reclassified into a habitat group other than their original habitat. These studies also presented behavioral and ecological explanations for these reclassifications. Table 2.11 lists those species in which over one half of the specimens were reclassified in a single analysis and table 2.12 lists those taxa where over one half of the specimens were reclassified in multiple analyses.

Of the 75 different species included in the analysis, only 10 had greater than one half of their individuals reclassified by more than one discriminant analysis. An additional 12 species had more than one half of their individuals reclassified in a single analysis. Plummer and Bishop (1994) found that complete discriminant function models were much more successful at classifying specimens by habitat than partial models. This appears to be only partly replicated here. Fewer specimens were misclassified in the complete analyses compared to the distal analyses overall but, among species where multiple analyses misclassified specimens, the distal analyses and complete analyses appeared equally unreliable. This result is likely attributable to two factors not present in Plummer and Bishop's (1994) study. First, Plummer and Bishop (1994) did not include species over 250 kg or mountain habitat specialists in their analyses. Negative allometry of metapodial length (see fig. 2.5) may explain reclassifications of large bovids such as

Syncerus caffer, *Bison bison,* and *Bubalis bubalis* into mountain or more closed habitats which are distinguished in part by relatively short metapodials. Second, Plummer and Bishop (1994) did not include mountain habitat specialists in their analysis. Since both closed habitat forms and mountain specialists have relatively short metapodials, reclassifications involving forest or heavy cover forms and mountain forms may account for some reclassification of specimens in complete analyses.

In addition to *Syncerus caffer* (both subspecies), and *Bison bison bison*, only *Kobus megaceros* was reclassified in more than one half of cases in both the complete metatarsal and complete metacarpal analyses. *Kobus megaceros* was also reclassified more than half the time in the distal metatarsal analysis. The complete metatarsal analysis reclassified specimens from heavy to light cover. Similarly, the complete metacarpal analysis and distal metatarsal analysis reclassified *Kobus megaceros* into the light cover and plains habitat groups. It has been suggested (Scott, 1979; Plummer & Bishop, 1994) that the hindlimbs of *Kobus megaceros* and other swamp dwelling bovids are adapted for speed and bounding. Such speed and bounding adaptations would be convergent with the adaptations for speed in plains and light cover bovids. Kappelman et al. (1997) suggested that the categorization of *Kobus megaceros* as a heavy cover bovid could be in error.

Madoqua guentheri was frequently reclassified in all the complete metatarsal analysis and the distal analyses from heavy cover to the plains or the light cover habitat group. *Madoqua guentheri* is very small in body size and poorly represented in the analysis (only three individuals). In particular, the small sample size available for *Madoqua guentheri* makes any interpretations regarding morphology and habitat uncertain. Similar results were obtained for *Madoqua guentheri* from previous analyses of the proximal femora (Kappelman et al., 1997; Scott et al., 1999). Specimens of *Madoqua kirki* were also frequently reclassified in more than one analysis. Thus, the

genus *Madoqua* performs particularly poorly and generally was reclassified into more open habitat categories. *Madoqua* appears tied to arid habitats with good cover and has an anti-predator strategy that employs both flight and alarm-calling or crypsis depending on the predator (Estes, 1991). Selection for arid habitat substrate and selection for efficient flight would appear to have been most significant selection pressures relevant to *Madoqua* metapodials.

Plummer and Bishop (1994) note frequent reclassifications for complete metacarpals of *Tragelaphus spekei* from intermediate to closed habitat and of *Hippotragus niger* from intermediate to open habitat. According to the five group habitat classification used in this study following Scott et al. (1999) and Kappelman et al. (1997), *Tragelaphus spekei* is placed in the heavy cover group while *Hippotragus niger* is placed in the light cover group. These classifications resulted in neither species being frequently reclassified. The more detailed classification used here appears to better correlate with the morphology of these two species.

Sylvicapra grimmia was reclassified from intermediate to closed habitat in the analysis of the complete metatarsal by Plummer and Bishop (1994). This result was not replicated here. However, the complete and distal metacarpal analyses resulted in frequent reclassifications. Plummer and Bishop (1994) suggested that reclassification of *Sylvicapra grimmia* was the result of either predator avoidance behavior that includes lying in tall grass to avoid predators or phylogeny as all other cephalophines are forest dwellers. However, the light cover category to which *Sylvicapra grimmia* was assigned explicitly includes tall grass (Kappelman et al., 1997). The phylogeny explanation is preferred here. It is important to note that of all the cephalophines, *Sylvicapra grimmia* had the scores farthest from the forest group mean on CV1 in the complete metacarpal analysis. The mean of CV1 (complete metacarpal) for *Sylvicapra grimmia* was -0.58 (*N* =

9) while the mean for all forest habitat specimens was 0.84 (N = 53). The other cephalophines had means for CV1 of 1.03 (*Cephalophus sylvicultor*, N = 7), 1.06 (*Cephalophus dorsalis*, N = 5), -0.40(*Cephalophus leucogaster*, N = 5), 0.47 (*Cephalophus weynsi*, N = 1), and 0.39 (*Philantomba monticola*, N = 1). Thus, despite being reclassified by the discriminant function for the complete metatarsal, it is quite clear that, given its phylogeny, *Sylvicapra grimmia*, has more open habitat type morphology. Indeed, the case of *Sylvicapra grimmia* and the other cephalophines is one of the clearest phylogenetic contrasts indicating that the morphology discussed here is linked to habitat and not better explained by phylogeny alone.

Antidorcas marsupialis, the springbok, was the only open habitat species frequently reclassified by Plummer and Bishop (1994) in both the distal metacarpal and distal metatarsal analyses. These reclassifications were not repeated in this study. The springbok is known to pronk (Estes, 1991), a specialized form of locomotion and display when all four feet contact the ground at the same time. The reclassifications for the springbok were attributed to pronking (Plummer & Bishop, 1994). However, no specific functional hypothesis has been suggested relating pronking to any morphology of the distal metapodials.

Tragelaphus scriptus, the bushbuck, was the only closed habitat species frequently reclassified by Plummer and Bishop (1994) in both the distal metacarpal and distal metatarsal analyses. The correct classification of the bushbuck is particularly important because it is one of the few non-cephalophines dependent on thick cover. The rate of reclassification for the bushbuck was lower in this study. In the case of the distal metatarsal, only two of 14 specimens were reclassified in this study. The results for the distal metacarpal (7 of 15 specimens reclassified) more closely resembled those of Plummer and Bishop (1994). Plummer and Bishop (1994) suggested that selection

pressure in ecotonal settings may account for reclassification of the bushbuck. The results of this study suggest that such selection pressures would most likely apply to the distal metacarpal.

In some cases, only a single individual of a species was available for analysis and this single individual was reclassified in one or more analyses. This was true for: *Gazella gazella*, *Alcelaphus lichtensteini, Kobus leche, Cephalophus weynsi*, *Bubalis bubalis*, *Neotragus batesi*, *Raphicerus sharpei*, and *Tragelaphus derbianus*. Post hoc interpretation of these results would have no real basis. Similarly, the specimens listed in Table 2.11 were reclassified in only a single analysis and post hoc interpretation should probably be limited.

Kobus ellipsiprymnus was frequently reclassified from heavy cover to light cover in the distal metatarsal analysis and frequently reclassified as light cover or plains in the complete metacarpal analysis (tab. 2.12). These reclassifications were mainly from one intermediate habitat category to another intermediate category. These results suggest that in intermediate habitats selection may operate differently on fore- and hindlimbs. Heavy cover results may be linked with a dependence on well-watered habitats while the light cover or plains results may be linked with a run-to-cover anti-predator strategy. This echoes the interpretation put forward by Plummer and Bishop (1994) for *Kobus ellipsiprymnus*.

Functional Morphology of Extant Bovids

Metapodial-Phalangeal Joint

Some support was found for the hypothesis that bovids from more closed habitats are more likely to splay the phalanges in extension. Significant results with respect to the variable rPOSINF (Kruskal-Wallis test: $p<0.001$) provide the best support for this

hypothesis in both metacarpals and metatarsals. Plains habitat bovids had reduced values for rPOSINF compared to forest and intermediate forms (tab. 2.7 & 2.8). A similar trend was also evident for POSANT in metacarpals. However, rINFANT displayed a contrasting trend in metatarsals. This later result suggests a potentially more complex pattern of phalangeal tracking with respect to habitat. It also appears that any relationship between habitat and the extent of phalangeal splaying is relatively weak as none of these three variables, all of which vary significantly across the five habitat groups, was included in the distal metapodial discriminant models.

The association between more railed verticilli and open habitats appears to be much stronger. For the metatarsal, rcLVAP, and rdMVAP were included in discriminant models. Similarly, rcLVAP, rdMVAP, and rdLVAP were included in metacarpal discriminant models. Generally, means for variables derived from LVAP and MVAP were larger for the plains habitat group compared to the forest habitat group (tab. 2.7 & 2.8). In the case of rcMVAP in metatarsals and metacarpals, the increasing monotonic trend from forest to heavy cover to light cover to plains provides clear quantitative support for more railed verticilli in more open habitat bovids. The results of this study appear to provide support for the functional hypothesis outlined earlier that open habitat bovids splay the phalanges less than other bovids and have more railed metapodial-phalangeal articulations. Support for the first part (phalangeal splaying) is more qualified but the second part (railed verticilli) is clear. With respect to this hypothesis, Köhler (1993) references a substrate specific model and the association of less railed metapodial verticilli with more closed environments is likely the result of moist substrates and wetter environments.

Metapodial Diaphysis

A second hypothesis links closed habitats to more medial-laterally expanded metapodial diaphyses. This particular condition could be proximately associated with multiple factors. For instance, Kappelman (1988) applied a model relating increased limb excursions from the parasagittal plane to winding paths in dense cover and decreased limb excursions to cursorial locomotion during flight from predators in open habitats. Accordingly, closed habitats would correspond to a more intense history of medial-lateral bending moments concentrated in the distal limb. The converse case of greater anterior-posterior bending moments in open habitat cursors would also appear likely. Thus, medial-lateral expansion of the metapodial diaphyses may be tied very closely to habitat cover. An alternative linkage between metapodial diaphysis shape and habitat might involve eccentric loading as a result of moist substrates. This later idea follows Gromova's (Gromova, 1949; Gromova, 1952) suggestion with respect to equids (see also Camp & Smith, 1942; Sondaar, 1968) and Köhler's (1993) general conceptualization of metapodial adaptation. Regardless of the precise proximate cause, an association between habitat and the extent of medial-lateral metapodial diaphyseal expansion is strongly supported.

The variable rcMML is a key component of the discriminant models for both the complete metacarpal and complete metatarsal and of all variables discussed here it apparently has the strongest association with habitat. A clear pattern of relatively reduced medial-lateral metapodial diaphyseal dimensions in open habitat bovids has already been described here (see tab. 2.7, figs. 2.6 & 2.7). Similarly, mountain habitat forms had larger values for rcMML, suggesting eccentric loads in difficult terrain result in selection pressures parallel to those in forested and/or wet habitats.

Metapodial Length

A third hypothesis links relatively long distal limbs with more open habitats. However, it is important to note that rcMLEN appears to have less discriminatory power relevant to habitat than rcMML. The idea that relative metapodial length is the most important correlate of habitat is not supported. Rather, diaphyseal shape as measured by rcMML appears to be a more important correlate of habitat.

Paleoenvironments

Pikermi

The fossil specimens from Pikermi suggest closed and humid habitats and these specimens clearly belong in either the forest or heavy cover habitat group. The distal analysis assigned the smaller specimen (YPM VP20693) to the forest group while the larger specimen (YPM VP20692) was placed in the heavy cover habitat group. This potentially suggests niche separation according to body size and habitat. However, the addition of the relative length variable rcMLEN in the complete analysis for YPM VP20693 resulted in a heavy cover classification as opposed to a forest classification. The longer metatarsal (higher value for rcMLEN) suggests the possibility of more rapid flight from predators and raises the possibility of a run to cover predator avoidance strategy in conjunction with a distal metatarsal with low values for rcMVAP indicative of adaptation for soft substrates in a humid habitat.

Body mass estimates derived from both specimens narrow their possible species identifications. The NOW mammal database (Neogene of the Old World: Database of fossil mammals, n.d.) was queried for species that would match the estimated body masses for both specimens. Such body mass estimates provide no certainty of species identification but should narrow the possibilities. In the absence of associated crania and

postcrania, an estimated body mass with all of its inherent problems (Fortelius et al., 1996) is probably the best evidence for a taxonomic match between crania and postcrania. The next best evidence would be a concordance between relative abundance of crania of a kind and postcrania of a kind. A final piece of evidence for matching crania and postcrania might be a finding of concordant adaptations. For instance, a metapodial classified unambiguously in the forest habitat might be expected to be a browser or at least a mixed feeder. This method has the pitfall of potentially eliminating consideration of novel adaptations and should probably be lent less weight than body size concordance or relative abundance concordance.

In the case of YPM VP20693 with an estimated body mass of 23 to 26 kg, *Gazella capricornis* (approx. 22 kg) and *Prostrepsiceros rotundicornis* (approx. 35 kg) had the closest estimated body masses. Both forms are mesodont and *Gazella capricornis* is reconstructed as a mixed feeder while *Prostrepsiceros rotundicornis* is considered a browser. One consistent interpretation of this evidence would be linking YPM VP20693 with *Gazella capricornis* which could be reconstructed as a humid area, broken habitat, run to cover, mixed feeder. Placing YPM VP20693 in *Prostrepsiceros rotundicornis* would potentially suggest a more forested habitat without the run-to-cover adaptation and a diet lacking the incorporation of graze.

The larger specimen, YPM VP20692, with an estimated body mass of about 161 kg might be attributed to various larger taxa from Pikermi including *Tragoportax amalthea* (approx. 127 kg), *Protoryx carolinae* (approx. 160 kg), and *Palaeoryx pallasi* (approx. 200 kg). *Paleoryx pallasi* is reconstructed as a grazer and may be the least consistent of these three taxa with YPM VP20693. Both *Tragoportax amalthea* and *Protoryx carolinae* are thought to be mixed feeders which is consistent with the classification of YPM VP20692 in the heavy cover habitat.

The most important result derived from a consideration of these two Pikermi specimens relates to the validation of the discriminant model for use with fossil taxa. The preponderant classification of Pikermi specimens in the forest and heavy cover groups for all phases of both the distal and complete analyses (tab. 2.10) is consistent with the body of scholarship concerning Pikermi. Solounias and Dawson-Saunders (1988) presented a strong critique of interpretations of Pikermi as an African savanna-like biome based largely on masticatory morphology. Instead, Pikermi is reconstructed as a sclerophyllous evergreen woodland (Solounias et al., 1999). This conclusion is consistent with the forest or heavy cover classifications here and supported by a concordance of alternate lines of evidence. These include $\delta^{13}C$ values from soil carbonate and tooth enamel indicative of C3 forests or woodlands (Quade et al., 1994) and paleobotanical evidence for the presence of sclerophyllous evergreen woodlands with chaparral undergrowth from various Miocene peri-Mediterranean localities (Axelrod, 1975). In general, a wide number of researchers support conclusions emphasizing the presence of woodlands in the peri-Mediterranean Miocene (Takhajan, 1957; Givulescu & Florei, 1960; Leopold, 1969; Benda, 1971; Raven, 1971; Benda & De Bruijn, 1982; Gregor, 1982; Salitova & Ramishvili, 1984; Kovar-Eder, 1987a; Kovar-Eder, 1987b; Bernor et al., 1990)

Thus, the analysis of metapodials from Pikermi provides an interpretation consistent with alternate lines of evidence. A possible criticism of the application of the methodology used here is the suggestion that fossil sites will reflect a predominantly primitive morphology rather than habitat-specific adaptations. This prediction can be falsified by findings of diverse morphotypes at different fossil sites and by results consistent with alternative lines of evidence. The case of Pikermi represents the latter finding and appears to validate application of the discriminant model developed here to

other sites. Even more importantly, results from other sites can be interpreted relative to Pikermi where multiple lines of paleoecological evidence have been well-applied.

Ballestar

The single metacarpal specimen from Ballestar suggests more open habitats than those present at Pikermi. The NOW mammal database includes a single bovid species at present, *Miotragocerus monacensis*, with an estimated body mass of 90 kg and a reconstructed diet of browse (Neogene of the Old World: Database of fossil mammals, n.d.). The classification of the IPS BA 20617 in the light cover group in the distal analysis (a habitat where some grazing would be a possibility) and lower body mass estimates for IPS BA 20617 (67 ×/÷1.72 based on MGSV) suggest the possibility that IPS BA 20617 could represent a species other than *Miotragocerus monacensis* or a female of a sexually dimorphic species.

Köhler (1993) referred to IPS BA 20617 to *Miotragocerus* sp. and classified it as a type A2 bovid – "wooded, very humid to semiaquatic habitats." Among extant bovids, Köhler (1993) considered *Tragelephas spekei* and *Cephalophus sylvicultor* type A2 bovids. According to the classification used here, *Tragelephas spekei* was put in the heavy cover group and *Cephalophus sylvicultor* was put in the forest group. The classification of IPS BA 20617 in either heavy cover or light cover category suggests habitats that were less closed or less wet than those in which *T. spekei* is found today.

Can Llobateres

Köhler (1993) reconstructed *Miotragocerus pannoniae* as a type A2 bovid adapted to "wooded, very humid to semiaquatic habitats." This reconstruction appears consistent with the classification of IPS CLL 20603 as an intermediate habitat bovid. The body mass estimates of 108 ×/÷1.72 kg and 99 ×/÷1.76 kg for IPS CLL 20603 exceed the

NOW database estimate of 80 kg for *Miotragocerus pannoniae* (NOW, n.d.). However, the difference in body mass estimates could be the result of individual variation.

Can Llobateres is possibly slightly younger than Ballestar and very near the MN 9/10 boundary with a C4Ar paleomagnetic correlation (Agusti et al., 2001; NOW, n.d.), while Ballestar appears to be an MN 9 locality (Agusti, 1982). Can Llobateres is best known for the presence of the hominoid *Dryopithecus* whose postcrania appear indicative of suspensory locomotion (Moyà-Solà & Köhler, 1996). In contrast, *Dryopithecus* appears to be absent from Ballestar. Both sites include species of *Miotragocerus* which have been reconstructed as water-dependent here and previously (Köhler, 1993). The results of the analyses presented here do not indicate any major difference between *Miotragocerus pannoniae* and *Miotragocerus* from Ballestar in terms of habitat preference. Can Ponsic also includes entries for both *Dryopithecus* and *Miotragocerus pannoniae* in the NOW database (Neogene of the Old World: Database of fossil mammals, n.d.). In contrast, Hostalets Pierola Superior, another Spanish MN 9 locality includes *Miotragocerus monacensis* but not *Dryopithecus*. The sampling of sites is low, but the apparent pattern is an association between *Miotragocerus pannoniae* and the hominoid *Dryopithecus*.

The only other bovid known from Can Llobateres is *Protragocerus chantrei* with a body mass of approximately 55 kg. (Neogene of the Old World: Database of fossil mammals, n.d.). Like *Miotragocerus pannoniae*, *Protragocerus chantrei* is reputed to be a browser (Neogene of the Old World: Database of fossil mammals, n.d.). No metapodials of *Protragocerus chantrei* are preserved from Can Llobateres and little can be said about it here. It is important to note that the best available species count of bovids for Can Llobateres is two and that *Protragocerus chantrei* may ultimately indicate greater habitat diversity at Can Llobateres.

IPS 2548 from Can Llobateres is attributed to the cervid *Amphiprox* and appeared to be either a light cover (complete analysis) or forest form (distal analysis) based on the antilocaprid-bovid comparative sample used here. The contrasting classifications for *Amphiprox* may well have to do with differential scaling of bovid and cervid metapodials. Further research is likely needed before cervids can confidently be incorporated in analyses such as this.

Torrent de Fibulines

The single complete specimen from Torrent de Fibulines, IPS 1237, is unique among Vallesian taxa in terms of its large body size. It has an estimated body mass that exceeds the largest estimated body masses recorded in the NOW database for Vallesian bovids and is more comparable to estimated body masses for different Turolian bovids (Neogene of the Old World: Database of fossil mammals, n.d.). Thus, IPS 1237 likely represents an undescribed large bovid.

The habitat classification for IPS 1237 was consistent for both the complete and distal metacarpal analyses and resulted in high probability classifications in the heavy cover habitat group. IPS 1237 appears to offer some evidence that heavy cover persisted during MN 10 in Spain and suggests the possibility of selection pressures for larger body size.

Y0496

The four metapodials studied here from the Chinji locality Y0496 add to a sample of bovid postcrania made up of three proximal femora from Y0496 (= “Y 35” in prior publications) (Kappelman, 1991; Scott et al., 1999). All three Y0496 proximal femora previously resulted in forest habitat classifications (Scott et al., 1999) which contrasts

with the intermediate and,(in one likely anomalous case) mountain habitat classifications for the four metapodials studied here.

These contrasting results suggest the possibility of mosaic evolution in bovid postcrania. Assuming that the few metapodials and femora available for study represent conspecifics, it would appear that femora and metapodials may have responded to different selection pressures. The adaptive significance of femoral head shape has been interpreted primarily in terms of predator avoidance strategy (Kappelman, 1988; Kappelman, 1991). In contrast, the distal metapodial may be subject to selection pressures determined more by substrate than predator avoidance strategy. The integration of femoral and metapodial results suggests a bovid less adapted for flight from predators but not tied to very wet habitats.

Y0076

Results from previous analyses of femora from Chinji locality Y0076 suggested a single forest-adapted bovid species with an estimated body mass ranging between 33 kg and 46 kg. Both distal metapodials analyzed here are consistent with this hypothesis in terms of size and likely habitat.

If distal metapodials are interpreted primarily as reflective of substrate adaptations and proximal femora as reflective of predator avoidance strategy as it relates to habitat cover, then the Y0076 bovid may have been tied to closed and wet environments. This would contrast with an earlier bovid from Y0496 potentially adapted to less wet substrates as indicated by its distal metapodials. This contrast could imply some temporal oscillation between wetter and drier conditions for Miocene Siwalik habitats.

Y0311

Scott et al. (1999) described six bovid eco-morphs from locality Y0311 based on a discriminant analysis of 15 femora and body mass estimates based on femoral head area. Two of these morphs were represented by single specimens and were the only specimens with estimated body masses below 30 kg. The remaining four morphs were split between the light cover and forest habitats and between two size groupings. Morphs 1 and 3 had body mass estimates from 38 kg to 62 kg and morphs 2 and 4 had body mass estimates from 80 to 86 kg. Morphs 1 and 2 were classified as forest forms while morphs 3 and 4 were classified as light cover forms. Thus, one hypothesis based on this data would split the majority of Y0311 bovids into four species based on habitat classification and body size.

Barry (pers. comm.) indicated that the majority of the Y0311 cranial specimens including horn cores may be assignable to two taxa of different sizes, a larger taxon, cf. *Selenoportax* sp. and a smaller taxon, cf. *Tragoceridus pilgrimi*. This would lead to an interpretation in which morphs 2 and 4 might be assigned to cf. *Selenoportax* sp. and morphs 1 and 3 might be assigned to cf. *Tragoceridus pilgrimi*. Both species would then appear to be morphologically diverse with respect to femoral characters relevant to habitat.

As with the femora discussed in Scott et al. (1999), the metapodial specimens could be placed in two size categories. The 38 kg to 60 kg size range based on femora from Y0311 appears consistent with the 49 kg to 64 kg size range based on metapodials from Y0311. It would appear that some or all of these specimens would belong to cf. *Tragoceridus pilgrimi*. Ten metapodials (three metatarsals and seven metacarpals) fall into this size group consistent with cf. *Tragoceridus pilgrimi*. The habitat classifications for these ten specimens were, however, diverse: three distal metacarpals were classified

in the forest group, two distal metacarpals were classified in the heavy cover group, and two distal metacarpals and three distal metatarsals were classified in the light cover group.

The larger femora from Y0311 (80-86 kg) likely correspond to the taxon or taxa represented by the larger metapodials from Y0311. The higher body mass estimates derived from these metapodials (101-142 kg) suggests a scaling relationship between femora and metapodials that differs to some degree from that more commonly observed in extant forms. Some or all of the larger femora and metapodials from Y0311 would appear to be assignable to cf. *Selenoportax* sp. These larger distal metapodials possibly of cf. *Selenoportax* sp. were classified into different habitat groups: two were classified in heavy cover, one was classified in light cover and the fourth (a metatarsal was classified in the mountain group with a low probability.

The metapodials from Y0311 do not appear to resolve questions concerning bovid species diversity at Y0311. The presence of two main size groupings according to both metapodials and femora supports the view apparently reflected by horn cores of two major bovid taxa at Y0311: 1) a smaller species, cf. *Tragoceridus pilgrimi*, and 2) a larger species, cf. *Selenoportax* sp. However, the great range of femoral head shapes for both size groupings of femora from Y0311 reported by Scott et al. (1999) makes a case for greater species diversity at Y0311. The diverse habitat classifications for metapodials of both size groups reported here makes it impossible to wholly reject this idea of greater species diversity.

"Time-averaging" is often invoked in paleontological contexts to explain high apparent intraspecific variation. In the case of Y0311, the presence of time-averaging would suggest the possibility that the Y0311 bovid assemblage samples a large enough time span to include a transition in habitat types. By this scenario, the differing habitat

classifications for specimens attributable to cf. *Tragoceridus pilgrimi* and cf. *Selenoportax* sp. would be the result of parallel cases of directional selection in response to changing habitat conditions. Similarly, variability in Femoral Head Shape Score (FHSS) (Scott et al., 1999) could be attributed to the same process.

This possibility may be supported by changes in relative taxonomic abundance following deposition at Y0311. Y0311 includes few equids (Scott et al., 1999) but is followed in time by localities with elevated equid abundance (Barry et al., 2002). Thus, changes leading to this "equid bulge" may be prefigured by variation in bovid morphology at Y0311. A similar change in relative abundance of equids and bovids appears likely in central Anatolia, Turkey at this same time (Scott et al., 2003) and such coincident timing suggests that these changes may be linked to global cooling between 10.9 and 9.8 Ma (Kennett, 1985; Kennett & Hodell, 1986; Kennett, 1995).

In general, the habitat classification results for metapodials from Y0311 range from forest to light cover. This result is consistent with the conclusions based on a previous analysis of bovid femora (Scott et al., 1999). These results confirm the possibility that a range of habitats would have been available to the hominoid *Sivapithecus parvada*. The classification results for metapodials reported here place a greater emphasis on intermediate type habitats (light and heavy cover) as opposed to forested habitats. These results are consistent with the inference made by Scott et al. (1999) of some habitat change between Chinji and Nagri times in the Siwaliks, possibly driven by global cooling. Since both Y0076 metapodials were classified in the forest group as discussed above, this trend also appears to be supported by the comparison of Y0076 with Y0311 which it precedes in time. However, Y0496 is older than both Y0076 and Y0311. As noted above, the metapodials from Y0496 do not appear to be

unequivocally forest-adapted. Bovids from Y0496 may have been tied to closed but less wet habitats.

Distal metapodials from Y0311 were more likely to result in intermediate classifications than the femora studied from Y0311. As noted previously, this apparent mosaic evolution may have an ecological interpretation. Intermediate habitat distal metapodials may suggest less wet substrate while femora classified in the forest habitat may indicate less reliance on flight from predators in open patches of habitat.

CONCLUSIONS

The validity of bovid metapodials as habitat indicators is supported by a large comparative data set of extant bovids. The discriminant method employed here included a crossvalidation step. Reclassifications of extant bovids based on discriminant functions remained robust with crossvalidation. This strong empirical basis for the use of bovid metapodials in habitat reconstructions of fossil sites is further supplemented by the successful application of the discriminant models developed here to metapodials from the comparatively well-understood site of Pikermi. Specimens from Pikermi were classified in the closed part of the habitat spectrum as predicted, based on a consensus view in which Pikermi is reconstructed as a sclerophyllous evergreen woodland.

Few specimens are available for analysis from the Miocene of Spain but two specimens attributed to the genus *Miotragocerus* were analyzed. These results do not suggest any distinction in terms of habitat for *Miotragocerus* at Can Llobateres versus *Miotragocerus* at Ballestar although the two may be distinct in size. The finding of a intermediate habitat bovid at Can Llobateres indicates a habitat consistent with suspensory adaptations in *Dryopithecus*. However, it does suggest that some open areas may have been present at Can Llobateres – possibly prefiguring the changes of the "mid-Vallesian crisis" in the direction of drier habitats (Agusti & Llenas, 2004). The single

bovid metapodial from Torrent de Fibulines suggests that heavy cover persisted into MN 10 times. The results from these Spanish sites are suggestive but sample sizes remain far from adequate. Hipparions are better represented at various Spanish Vallesian sites and may help resolve the paleoenvironments at these sites.

Scott et al. (1999) concluded that a diversity of habitats may have been available to the hominoid, *Sivapithecus parvada*, at Y0311. This conclusion is supported by the discriminant analysis of bovid metapodials discussed here. Distal metapodials from Y0311 appear to largely fall in the two intermediate habitat categories, while previous work on Y0311 bovid femora placed more emphasis on the forest habitat category. Taken collectively, the evidence relevant to the paleoenvironment of *Sivapithecus parvada* at Y0311 suggests the presence of closed canopies at Y0311 as well as more lightly wooded areas. Diverse and intermediate morphology among Y0311 bovids may have resulted from the same ecological factors tied to a rise in equid relative abundance immediately following 10 Ma.

The fossil sample available for use in ecological reconstruction is typically small. A full understanding of the diversity of habitats available to Miocene hominoids will be improved as more fossils are discovered. Y0311 appears to have potentially presented an array of habitats (including light cover possibly later exploited by equids) to *Sivapithecus parvada*. Can Llobateres is poorly sampled but likely included habitats with intermediate cover used by *Miotragocerus*.

It is possible that Y0311 in the east included more diverse habitats than Can Llobateres in the west. The metapodial sample from Can Llobateres and Ballestar is too small to allow a definitive assessment of bovid diversity at these sites although the NOW database (Neogene of the Old World: Database of fossil mammals, n.d.) records two bovid species at Can Llobateres and one at Ballestar. This contrasts with from two to four

bovid species from Y0311. Regardless of precise bovid species diversity at Y0311 the metapodial sample suggests a range of habitats. In contrast, Can Llobateres may be dominated by *Miotragocerus pannoniae* and the metacarpal attributed to *Miotragocerus pannoniae* from Can Llobateres suggests an intermediate habitat. A hypothesis associating hominoids with greater habitat diversity in the east than in the west deserves further study.

Table 2.1: Measurements taken.

Short Description	Abbreviation	Measurement Type	Analogous Equid Measurement
maximum length	MLEN	length	M1
functional length	FLEN[1]	length	M2
proximal articulation, mediolateral	PML	proximal epiphysis	M5
proximal articulation, anteroposterior	PAP	proximal epiphysis	M6
midshaft, mediolateral	MML[2]	diaphysis	M3
midshaft, anteroposterior	MAP[2]	diaphysis	M4
posterior naviculocuboid facet, mediolateral	PNML[3,4]	proximal epiphysis	
magnum facet, mediolateral	MGML[5]	proximal epiphysis	
proximal quartile, mediolateral	PQML[2]	diaphysis	
proximal quartile, anteroposterior	PQAP[2]	diaphysis	
distal quartile, mediolateral	DQML[2]	diaphysis	
distal quartile, anteroposterior	DQAP[2]	diaphysis	
external margin medial trochlea, anteroposterior	EMAP	distal epiphysis	M14
medial verticilli, anteroposterior	MVAP	distal epiphysis	M12
internal margin medial trochlea, anteroposterior	IMAP	distal epiphysis	
external margin lateral trochlea, anteroposterior	ELAP	distal epiphysis	
lateral verticilli, anteroposterior	LVAP	distal epiphysis	M12
internal margin lateral trochlea, anteroposterior	ILAP	distal epiphysis	M13
anterior (cranial or dorsal) aspect verticilli, mediolateral	AVML	distal epiphysis	
inferior (distal) aspect verticilli, mediolateral	IVML	distal epiphysis	
posterior (caudal or palmar) aspect verticilli, mediolateral	PVML	distal epiphysis	
anterior (cranial or dorsal) aspect distal articulation, mediolateral	ADML	distal epiphysis	
inferior (distal) aspect distal articulation, mediolateral	IDML	distal epiphysis	M11
posterior (caudal or palmar) aspect distal articulation, mediolateral	PDML	distal epiphysis	
distal diaphysis, mediolateral	DDML	diaphysis	M10
distal diaphysis, anteroposterior	DDAP	diaphysis	
distal epiphysis, mediolateral	DEML[5]	distal epiphysis	
distal epiphysis, anteroposterior	DEAP[5]	distal epiphysis	
inferior aspect intratrochlear, mediolateral	IIML	distal epiphysis	

[1]medial length of MT and lateral length of MC; [2]midshaft and quartiles determined using functional length; [3]after Plummer and Bishop, 1994; [4]metatarasal only; [5]metacarpal only; [6]after Scott, 1990

Table 2.2: Size variables used.

Size Variable	Equation
Metapodial Global Size Variable (MGSV)	$= \sqrt[9]{PML \bullet PAP \bullet MML \bullet MAP \bullet EMAP \bullet ILAP \bullet IDML \bullet DDML \bullet \sqrt{MVAP \bullet LVAP}}$
Distal Metapodial Global Size Variable (DMGSV)	$= \sqrt[5]{EMAP \bullet ILAP \bullet IDML \bullet DDML \bullet \sqrt{MVAP \bullet LVAP}}$

Table 2.3: Least squares regression statistics for species means of body mass versus MGSV and DMGSV.

Independent Variable	Element	Intercept	Slope	*df*	R^2	*P*	95% Confidence Interval of the Slope	95% Confidence Interval of the Intercept
MGSV	MT	-2.31491	3.097667	81	0.9753	< 0.0001	2.9887 - 3.2066	-2.4626 --2.1672
MGSV	MC	-1.85403	2.800343	99	0.9600	< 0.0001	2.6864 - 2.9143	-2.0064 --1.7017
DMGSV	MT	-2.34421	3.101925	81	0.9747	< 0.0001	2.9914 - 3.2125	-2.4949 --2.1936
DMGSV	MC	-1.91335	2.796082	99	0.9547	< 0.0001	2.6746 - 2.9176	-2.0786 --1.7481

Table 2.4: Least squares regression statistics for morphological variables versus size.

Analysis	Element	Variable	Intercept	Slope	*df*	R^2	*P*	95% Confidence Interval of the Slope	95% Confidence Interval of the Intercept
complete	MT	cMLEN	1.4511	-0.3715	337	0.3834	<0.0001	-0.422 - -0.321	1.3828 - 1.5194
complete	MT	cPML	0.0726	0.0093	337	0.0055	0.1737	-0.0041 - 0.0226	0.0545 - 0.0907
complete	MT	cPAP	0.1045	-0.0146	337	0.0115	0.0480	-0.029 - -0.0001	0.085 - 0.1241
complete	MT	cMML	-0.1519	0.0315	337	0.0187	0.0117	0.0071 -0.056	-0.185 - -0.1188
complete	MT	cMAP	-0.0759	-0.0132	337	0.0056	0.1708	-0.0321 - 0.0057	-0.1015 - -0.0503
complete	MT	cPNML	-0.5103	0.1053	323	0.0294	0.0019	0.0391 - 0.1715	-0.6001 - -0.4205
complete	MT	cPQML	-0.1481	0.0239	337	0.0094	0.0746	-0.0024 - 0.0502	-0.1836 - -0.1125
complete	MT	cPQAP	-0.0468	0.0028	337	0.0002	0.8076	-0.0199 - 0.0255	-0.0774 - -0.0161
complete	MT	cDQML	-0.3278	0.2005	337	0.2757	<0.0001	0.1657 - 0.2354	-0.3749 - -0.2806
complete	MT	cDQAP	-0.1766	0.0227	337	0.0180	0.0134	0.0047 - 0.0407	-0.2009 - -0.1522
complete	MT	cEMAP	-0.1050	-0.0310	337	0.0299	0.0014	-0.05 - -0.0121	-0.1306 - -0.0794
complete	MT	cMVAP	0.0820	-0.0730	337	0.3292	<0.0001	-0.0842 - -0.0618	0.0669 - 0.0971
complete	MT	cIMAP	0.0281	-0.0749	337	0.3463	<0.0001	-0.0859 - -0.0639	0.0132 -0.043
complete	MT	cELAP	-0.0664	-0.0810	337	0.1524	<0.0001	-0.1015 - -0.0605	-0.0941 - -0.0387
complete	MT	cLVAP	0.0860	-0.0838	337	0.3895	<0.0001	-0.095 - -0.0725	0.0708 - 0.1012
complete	MT	cILAP	0.0018	-0.0513	337	0.2118	<0.0001	-0.0619 - -0.0407	-0.0125 - 0.0162
complete	MT	cAVML	-0.2402	0.0311	337	0.0141	0.0289	0.0032 -0.059	-0.2779 - -0.2024
complete	MT	cIVML	-0.2713	0.0764	337	0.0884	<0.0001	0.0501 - 0.1027	-0.3069 - -0.2357
complete	MT	cPVML	-0.1789	0.0320	337	0.0242	0.0041	0.0102 - 0.0538	-0.2084 - -0.1494
complete	MT	cADML	-0.0108	0.0435	337	0.0379	0.0003	0.02 - 0.0669	-0.0426 -0.021
complete	MT	cIDML	0.0180	0.0824	337	0.1486	<0.0001	0.0613 - 0.1035	-0.0106 - 0.0466
complete	MT	cPDML	0.0374	0.0688	336	0.1233	<0.0001	0.0491 - 0.0885	0.0108 - 0.0641
complete	MT	cPDML	0.0374	0.0688	336	0.1233	<0.0001	0.0491 - 0.0885	0.0108 - 0.0641
complete	MT	cDDML	0.0518	0.0652	337	0.1778	<0.0001	0.0502 - 0.0803	0.0315 - 0.0722
complete	MT	cDDAP	-0.0085	-0.0363	337	0.0307	0.0012	-0.0581 - -0.0144	-0.0381 -0.021
complete	MT	cDEML	0.0054	0.0909	336	0.2064	<0.0001	0.0718 - 0.1101	-0.0205 - 0.0313
complete	MT	cDEML	0.0054	0.0909	336	0.2064	<0.0001	0.0718 - 0.1101	-0.0205 - 0.0313
complete	MT	cDEAP	-0.0922	-0.0173	337	0.0047	0.2070	-0.0442 - 0.0096	-0.1286 - -0.0558
complete	MT	cIIML	-0.7887	-0.0812	337	0.0266	0.0026	-0.1337 - -0.0286	-0.8598 - -0.7175
complete	MC	cMLEN	1.5093	-0.4335	334	0.3961	<0.0001	-0.4911 - -0.3759	1.4321 - 1.5865
complete	MC	cPML	0.1054	0.0308	334	0.0371	0.0004	0.0139 - 0.0476	0.0828 -0.128
complete	MC	cPAP	0.0305	-0.0553	334	0.1381	<0.0001	-0.0701 - -0.0404	0.0106 - 0.0504
complete	MC	cMML	-0.1354	0.0546	334	0.0572	<0.0001	0.0307 - 0.0784	-0.1674 - -0.1034
complete	MC	cMAP	-0.1061	-0.0330	334	0.0343	0.0007	-0.0519 - -0.0142	-0.1314 - -0.0808
complete	MC	cMGML	-0.0309	0.0019	334	0.0001	0.8628	-0.0199 - 0.0238	-0.0602 - -0.0016
complete	MC	cPQML	-0.1736	0.0898	334	0.1332	<0.0001	0.0651 - 0.1144	-0.2066 - -0.1405
complete	MC	cPQAP	-0.1026	-0.0160	334	0.0080	0.1018	-0.0351 - 0.0032	-0.1282 - -0.0769
complete	MC	cDQML	-0.2371	0.1756	334	0.2332	<0.0001	0.1413 - 0.2098	-0.283 - -0.1911
complete	MC	cDQAP	-0.1909	0.0073	334	0.0013	0.5116	-0.0145 - 0.0291	-0.2201 - -0.1616

complete	MC	cEMAP	-0.0782	-0.0382	334	0.0343	0.0007	-0.06 - -0.0164	-0.1074 - -0.0489
complete	MC	cMVAP	0.0669	-0.0600	334	0.2003	<0.0001	-0.0729 - -0.0471	0.0497 - 0.0842
complete	MC	cIMAP	0.0252	-0.0635	334	0.2038	<0.0001	-0.077 - -0.05	0.0071 - 0.0433
complete	MC	cELAP	-0.0478	-0.0740	334	0.0935	<0.0001	-0.0988 - -0.0492	-0.081 - -0.0146
complete	MC	cLVAP	0.0806	-0.0732	334	0.2625	<0.0001	-0.0864 - -0.06	0.0629 - 0.0983
complete	MC	cILAP	0.0226	-0.0575	334	0.1598	<0.0001	-0.0717 - -0.0433	0.0036 - 0.0416
complete	MC	cAVML	-0.2437	0.0334	334	0.0200	0.0094	0.0083 - 0.0585	-0.2773 - -0.21
complete	MC	cIVML	-0.2701	0.0845	334	0.1213	<0.0001	0.06 - 0.1089	-0.3028 - -0.2373
complete	MC	cPVML	-0.1780	0.0385	334	0.0395	0.0002	0.0181 -0.059	-0.2053 - -0.1506
complete	MC	cADML	0.0050	0.0469	334	0.0449	0.0001	0.0236 - 0.0701	-0.0261 - 0.0362
complete	MC	cIDML	0.0254	0.0945	334	0.2051	<0.0001	0.0745 - 0.1146	-0.0014 - 0.0522
complete	MC	cPDML	0.0219	0.0912	334	0.1909	<0.0001	0.071 - 0.1115	-0.0052 - 0.0489
complete	MC	cDDML	0.0620	0.0707	334	0.1967	<0.0001	0.0553 - 0.0861	0.0414 - 0.0826
complete	MC	cDDAP	-0.0294	-0.0351	334	0.0333	0.0008	-0.0555 - -0.0147	-0.0567 - -0.0021
complete	MC	cDEML	-0.0085	0.1115	334	0.3015	<0.0001	0.0932 - 0.1298	-0.033 - 0.0159
complete	MC	cDEAP	-0.1200	0.0069	334	0.0014	0.4975	-0.0132 - 0.0271	-0.147 - -0.0931
complete	MC	cIIML	-0.8612	-0.0568	334	0.0118	0.0467	-0.1127 - -0.0008	-0.9362 - -0.7862
distal	MT	INFANT	-0.0333	0.0467	338	0.0673	<0.0001	0.0281 - 0.0653	-0.0586 - -0.008
distal	MT	POSANT	0.0610	0.0011	338	0.0000	0.9142	-0.0186 - 0.0208	0.0342 - 0.0878
distal	MT	POSINF	0.0944	-0.0456	338	0.1175	<0.0001	-0.059 - -0.0323	0.0762 - 0.1125
distal	MT	dEMAP	-0.1141	-0.0290	338	0.0279	0.0020	-0.0473 - -0.0107	-0.139 - -0.0893
distal	MT	dMVAP	0.0706	-0.0691	338	0.4001	<0.0001	-0.0782 - -0.0601	0.0583 - 0.0829
distal	MT	dIMAP	0.0187	-0.0725	338	0.3662	<0.0001	-0.0827 - -0.0623	0.0048 - 0.0326
distal	MT	dELAP	-0.0763	-0.0782	338	0.1504	<0.0001	-0.0981 - -0.0583	-0.1033 - -0.0493
distal	MT	dLVAP	0.0751	-0.0802	338	0.4389	<0.0001	-0.0899 - -0.0705	0.0619 - 0.0883
distal	MT	dILAP	-0.0066	-0.0497	338	0.2038	<0.0001	-0.0602 - -0.0392	-0.0209 - 0.0077
distal	MT	dAVML	-0.2521	0.0348	338	0.0186	0.0118	0.0078 - 0.0619	-0.2889 - -0.2153
distal	MT	dIVML	-0.2854	0.0816	338	0.1117	<0.0001	0.0569 - 0.1062	-0.3189 - -0.252
distal	MT	dPVML	-0.1911	0.0359	338	0.0336	0.0007	0.0153 - 0.0565	-0.2191 - -0.163
distal	MT	dADML	-0.0221	0.0467	338	0.0464	0.0001	0.0241 - 0.0694	-0.0529 - 0.0087
distal	MT	dIDML	0.0054	0.0864	338	0.1803	<0.0001	0.0667 - 0.1061	-0.0213 - 0.0322
distal	MT	dPDML	0.0267	0.0716	337	0.1430	<0.0001	0.0528 - 0.0904	0.0012 - 0.0522
distal	MT	dDDML	0.0425	0.0670	338	0.1869	<0.0001	0.052 - 0.0819	0.0222 - 0.0628
distal	MT	dDDAP	-0.0125	-0.0380	338	0.0301	0.0013	-0.0611 - -0.0149	-0.0439 - 0.0189
distal	MT	dDEML	-0.0045	0.0929	337	0.2214	<0.0001	0.0743 - 0.1116	-0.0299 - 0.0209
distal	MT	dDEAP	-0.1002	-0.0160	338	0.0042	0.2340	-0.0425 - 0.0104	-0.1362 - -0.0643
distal	MT	dIIML	-0.8086	-0.0712	338	0.0213	0.0070	-0.1228 - -0.0196	-0.8787 - -0.7384
distal	MC	INFANT	-0.0284	0.0517	334	0.1315	<0.0001	0.0374 -0.066	-0.0478 - -0.0089
distal	MC	POSANT	0.0661	0.0048	334	0.0012	0.5351	-0.0105 - 0.0202	0.0452 - 0.0869
distal	MC	POSINF	0.0944	-0.0469	334	0.1591	<0.0001	-0.0585 - -0.0353	0.0786 - 0.1102
distal	MC	dEMAP	-0.1036	-0.0350	334	0.0372	0.0004	-0.0541 - -0.0158	-0.1297 - -0.0775
distal	MC	dMVAP	0.0441	-0.0583	334	0.2926	<0.0001	-0.0681 - -0.0486	0.0308 - 0.0574
distal	MC	dIMAP	0.0034	-0.0625	334	0.2640	<0.0001	-0.0737 - -0.0513	-0.0119 - 0.0187
distal	MC	dELAP	-0.0727	-0.0706	334	0.1023	<0.0001	-0.0932 - -0.0481	-0.1033 - -0.042
distal	MC	dLVAP	0.0584	-0.0717	334	0.3533	<0.0001	-0.0822 - -0.0613	0.0441 - 0.0726
distal	MC	dILAP	0.0005	-0.0565	334	0.2054	<0.0001	-0.0684 - -0.0445	-0.0158 - 0.0168
distal	MC	dAVML	-0.2621	0.0303	334	0.0158	0.0212	0.0046 -0.056	-0.2971 - -0.2271

distal	MC	dIVML	-0.2905	0.0820	334	0.1128	<0.0001	0.0572 - 0.1067	-0.3242 - -0.2568
distal	MC	dPVML	-0.1961	0.0351	334	0.0303	0.0014	0.0137 - 0.0565	-0.2252 - -0.167
distal	MC	dADML	-0.0132	0.0433	334	0.0361	0.0005	0.0192 - 0.0675	-0.046 - 0.0196
distal	MC	dIDML	0.0067	0.0906	334	0.1738	<0.0001	0.0694 - 0.1119	-0.0223 - 0.0357
distal	MC	dPDML	0.0049	0.0861	334	0.1491	<0.0001	0.064 - 0.1083	-0.0253 -0.035
distal	MC	dDDML	0.0451	0.0658	334	0.1386	<0.0001	0.0482 - 0.0835	0.0211 - 0.0692
distal	MC	dDDAP	-0.0471	-0.0376	334	0.0364	0.0004	-0.0584 - -0.0168	-0.0755 - -0.0188
distal	MC	dDEML	-0.0258	0.1062	334	0.2376	<0.0001	0.0858 - 0.1267	-0.0537 - 0.0021
distal	MC	dDEAP	-0.1404	0.0057	334	0.0010	0.5709	-0.0141 - 0.0255	-0.1674 - -0.1135
distal	MC	dIIML	-0.8766	-0.0607	334	0.0133	0.0348	-0.117 - -0.0044	-0.9533 - -0.8

Table 2.5: Statistics for Kruskal-Wallis tests and stepwise discriminant analyses.

			Kruskal-Wallis Test			Stepwise Discriminant Analysis			
Analysis	**Element**	**Variable**	***df***	χ^2	***P***	**Step**	**Wilks' lambda**	***F***	***P***
complete	MT	rcMLEN	4	126.4	<.001	4	0.1740	26.72	<.0001
complete	MT	cPML	4	29.7	<.001	24	0.0649	11.52	<.0001
complete	MT	rcMML	4	170.5	<.001	1	0.5361	71.83	<.0001
complete	MT	rcPAP	4	92.9	<.001	21	0.0759	0.93	0.4479
complete	MT	cMAP	4	80.8	<.001	23	0.0746	0.53	0.7173
complete	MT	rcPNML	4	68.4	<.001	n/a			
complete	MT	cPQML	4	164.6	<.001	7	0.1156	4.4	0.0018
complete	MT	cPQAP	4	80.8	<.001	8	0.1109	3.49	0.0083
complete	MT	rcDQML	4	153.1	<.001	10	0.1018	2.9	0.0221
complete	MT	rcDQAP	4	105.9	<.001	17	0.0802	1.4	0.2347
complete	MT	rcEMAP	4	63.1	<.001	12	0.0943	3.41	0.0095
complete	MT	rcMVAP	4	76.9	<.001	13	0.0887	5.03	0.0006
complete	MT	rcIMAP	4	47.7	<.001	25	0.0645	0.47	0.7588
complete	MT	rcELAP	4	59.3	<.001	11	0.0983	2.86	0.0235
complete	MT	rcLVAP	4	40.9	<.001	3	0.2306	40.1	<.0001
complete	MT	rcILAP	4	43.4	<.001	9	0.1054	4.18	0.0026
complete	MT	rcAVML	4	67.2	<.001	16	0.0816	2.12	0.0784
complete	MT	rcIVML	4	109.0	<.001	22	0.0751	0.87	0.4816
complete	MT	rcPVML	4	69.8	<.001	19	0.0778	1.09	0.3633
complete	MT	rcADML	4	88.0	<.001	14	0.0857	2.78	0.027
complete	MT	rcIDML	4	106.8	<.001	2	0.3427	46.7	<.0001
complete	MT	rcPDML	4	86.7	<.001	26	0.0642	0.39	0.8126
complete	MT	rcDDML	4	95.3	<.001	5	0.1450	16.43	<.0001
complete	MT	rcDDAP	4	96.4	<.001	6	0.1219	15.51	<.0001
complete	MT	rcDEML	4	74.9	<.001	18	0.0788	1.38	0.2421
complete	MT	cDEAP	4	5.8	0.217	20	0.0768	0.98	0.4211
complete	MT	rcIIML	4	79.7	<.001	15	0.0838	1.81	0.1258
complete	MC	rcMLEN	4	124.0	<.001	8	0.1250	11.01	<.0001
complete	MC	rcPML	4	4.9	0.299	not entered			>.99
complete	MC	rcPAP	4	10.9	0.027	24	0.0690	0.75	0.5591
complete	MC	rcMML	4	155.5	<.001	1	0.5491	67.96	<.0001
complete	MC	rcMAP	4	52.3	<.001	18	0.0756	1.75	0.1381
complete	MC	cMGML	4	67.0	<.001	11	0.0997	4.39	0.0018
complete	MC	rcPQML	4	141.9	<.001	14	0.0855	3.3	0.0113
complete	MC	cPQAP	4	55.8	<.001	19	0.0741	1.51	0.1979
complete	MC	rcDQML	4	105.3	<.001	20	0.0729	1.35	0.2497
complete	MC	cDQAP	4	48.8	<.001	23	0.0697	0.97	0.4237
complete	MC	rcEMAP	4	106.7	<.001	6	0.1686	14.42	<.0001
complete	MC	rcMVAP	4	71.7	<.001	15	0.0822	3.16	0.0145

complete	MC	rcIMAP	4	81.2	<.001	16	0.0793	2.83	0.0248
complete	MC	rcELAP	4	94.4	<.001	21	0.0715	1.48	0.2068
complete	MC	rcLVAP	4	64.4	<.001	4	0.2428	16.69	<.0001
complete	MC	rcILAP	4	99.5	<.001	22	0.0706	1.03	0.3899
complete	MC	rcAVML	4	107.7	<.001	2	0.3481	47.63	<.0001
complete	MC	rcIVML	4	95.8	<.001	13	0.0890	5.67	0.0002
complete	MC	rcPVML	4	72.8	<.001	25	0.0684	0.73	0.571
complete	MC	rcADML	4	94.2	<.001	7	0.1420	15.21	<.0001
complete	MC	rcIDML	4	87.0	<.001	10	0.1052	8.4	<.0001
complete	MC	rcPDML	4	77.4	<.001	17	0.0773	2.12	0.0781
complete	MC	rcDDML	4	109.7	<.001	5	0.1984	18.29	<.0001
complete	MC	rcDDAP	4	79.6	<.001	3	0.2922	15.72	<.0001
complete	MC	rcDEML	4	68.0	<.001	9	0.1162	6.14	<.0001
complete	MC	cDEAP	4	22.2	<.001	26	0.0673	1.18	0.3205
complete	MC	rcIIML	4	81.6	<.001	12	0.0953	3.69	0.0059
distal	MT	rINFANT	4	18.4	0.001	not entered			>.99
distal	MT	POSANT	4	1.9	0.757	11	0.1618	1.2	0.3103
distal	MT	rPOSINF	4	38.5	<.001	not entered			>.99
distal	MT	rdEMAP	4	71.9	<.001	1	0.6360	47.65	<.0001
distal	MT	rdMVAP	4	51.4	<.001	3	0.3525	26.8	<.0001
distal	MT	rdIMAP	4	52.7	<.001	17	0.1426	0.38	0.8207
distal	MT	rdELAP	4	60.6	<.001	6	0.1954	11.04	<.0001
distal	MT	rdLVAP	4	23.8	<.001	13	0.1465	1.15	0.3312
distal	MT	rdILAP	4	83.9	<.001	5	0.2217	11.08	<.0001
distal	MT	rdAVML	4	47.5	<.001	10	0.1642	1.81	0.1274
distal	MT	rdIVML	4	86.0	<.001	14	0.1452	0.69	0.6004
distal	MT	rdPVML	4	53.2	<.001	12	0.1486	7.16	<.0001
distal	MT	rdADML	4	55.0	<.001	7	0.1794	7.25	<.0001
distal	MT	rdIDML	4	74.5	<.001	4	0.2515	33.11	<.0001
distal	MT	rdPDML	4	72.4	<.001	8	0.1729	3.1	0.0159
distal	MT	rdDDML	4	98.8	<.001	not entered			>.99
distal	MT	rdDDAP	4	122.6	<.001	2	0.4667	30.12	<.0001
distal	MT	rdDEML	4	58.8	<.001	16	0.1432	0.5	0.7322
distal	MT	dDEAP	4	12.7	0.013	15	0.1442	0.59	0.6729
distal	MT	rdIIML	4	72.0	<.001	9	0.1678	2.43	0.0473
distal	MC	rINFANT	4	10.5	0.033	16	0.1135	0.63	0.641
distal	MC	POSANT	4	33.5	<.001	11	0.1311	3.78	0.0051
distal	MC	rPOSINF	4	47.3	<.001	17	0.1002	10.41	<.0001
distal	MC	rdEMAP	4	97.7	<.001	1	0.5542	66.56	<.0001
distal	MC	rdMVAP	4	38.3	<.001	3	0.2893	22.85	<.0001
distal	MC	rdIMAP	4	66.7	<.001	10	0.1372	3.95	0.0038
distal	MC	rdELAP	4	90.1	<.001	14	0.1175	2.18	0.0708
distal	MC	rdLVAP	4	45.1	<.001	9	0.1440	6.05	0.0001
distal	MC	rdILAP	4	89.0	<.001	12	0.1262	3.09	0.0162
distal	MC	rdAVML	4	91.6	<.001	not entered			>.99
distal	MC	rdIVML	4	77.9	<.001	7	0.1650	7.97	<.0001
distal	MC	rdPVML	4	70.0	<.001	not entered			>.99

distal	MC	rdADML	4	75.5	<.001	4	0.2365	18.28	<.0001
distal	MC	rdIDML	4	76.4	<.001	not entered			>.99
distal	MC	rdPDML	4	83.3	<.001	15	0.1144	2.16	0.0735
distal	MC	rdDDML	4	123.2	<.001	5	0.1971	16.38	<.0001
distal	MC	rdDDAP	4	107.1	<.001	2	0.3696	41.21	<.0001
distal	MC	rdDEML	4	82.5	<.001	6	0.1811	7.16	<.0001
distal	MC	dDEAP	4	20.6	<.001	13	0.1208	3.58	0.0071
distal	MC	rdIIML	4	79.4	<.001	8	0.1547	5.34	0.0004

Table 2.6A: Complete metatarsal discriminant function analysis classification accuracy with and (without) crossvalidation.

Actual group	***N***	**Forest**	**Heavy cover**	**Light cover**	**Plains**	**Mountain**	**Percent correct**	**BTC**	**Q**
.	339	.	.	.	.	.	70.5 (81.7)	3.5 (4.1)	540.37 (806.87)
Forest	52	44 (51)	5 (0)	1 (0)	1 (0)	1 (1)	84.6 (98.1)	4.2 (4.9)	135.69 (198.12)
Heavy cover	64	2 (2)	41 (47)	16 (12)	3 (1)	2 (2)	64.1 (73.4)	3.2 (3.7)	77.66 (114.22)
Light cover	89	4 (4)	20 (12)	50 (63)	12 (7)	3 (3)	56.2 (70.8)	2.8 (3.5)	72.81 (143.47)
Plains	94	1 (0)	5 (4)	14 (11)	71 (78)	3 (1)	75.5 (83)	3.8 (4.1)	181.17 (233.02)
Mountain	40	2 (1)	2 (0)	2 (0)	1 (1)	33 (38)	82.5 (95)	4.1 (4.8)	97.66 (140.63)

Table 2.6B: Complete metacarpal discriminant function analysis classification accuracy with and (without) crossvalidation.

Actual group	***N***	**Forest**	**Heavy cover**	**Light cover**	**Plains**	**Mountain**	**Percent correct**	**BTC**	**Q**
.	336	.	.	.	.	.	67.6 (77.7)	3.4 (3.9)	475 (698.63)
Forest	53	38 (46)	12 (7)	2 (0)	0 (0)	1 (0)	71.7 (86.8)	3.6 (4.3)	88.53 (147.78)
Heavy cover	64	9 (8)	35 (40)	11 (9)	7 (7)	2 (0)	54.7 (62.5)	2.7 (3.1)	48.13 (72.25)
Light cover	91	11 (10)	13 (7)	54 (63)	10 (8)	3 (3)	59.3 (69.2)	3 (3.5)	88.02 (137.85)
Plains	88	2 (2)	4 (2)	13 (5)	68 (78)	1 (1)	77.3 (88.6)	3.9 (4.4)	180.41 (259.1)
Mountain	40	1 (1)	3 (1)	1 (1)	3 (3)	32 (34)	80 (85)	4 (4.3)	90 (105.63)

Table 2.6C: Distal metatarsal discriminant function analysis classification accuracy with and (without) crossvalidation.

Actual group	***N***	**Forest**	**Heavy cover**	**Light cover**	**Plains**	**Mountain**	**Percent correct**	**BTC**	**Q**
.	340	.	.	.	.	.	66.2 (77.6)	3.3 (3.9)	453.11 (706.18)
Forest	52	41 (47)	10 (4)	0 (0)	0 (0)	1 (1)	78.8 (90.4)	3.9 (4.5)	112.54 (161)
Heavy cover	64	7 (6)	32 (39)	15 (10)	9 (9)	1 (0)	50 (60.9)	2.5 (3)	36 (67.04)
Light cover	90	7 (5)	14 (10)	49 (58)	18 (15)	1 (1)	54.4 (64.4)	2.7 (3.2)	66.74 (111.11)
Plains	94	0 (0)	5 (3)	14 (7)	69 (81)	6 (3)	73.4 (86.2)	3.7 (4.3)	167.56 (257.24)
Mountain	40	1 (1)	1 (0)	1 (0)	3 (0)	34 (39)	85 (97.5)	4.3 (4.9)	105.63 (150.16)

Table 2.6D: Distal metacarpal discriminant function analysis classification accuracy with and (without) crossvalidation.

Actual group	*N*	Forest	Heavy cover	Light cover	Plains	Mountain	Percent correct	BTC	Q
.	336	.	.	.	.	.	62.5 (76.2)	3.1 (3.8)	379.31 (663.05)
Forest	53	37 (44)	10 (7)	4 (2)	0 (0)	2 (0)	69.8 (83)	3.5 (4.2)	82.19 (131.55)
Heavy cover	64	7 (6)	35 (46)	11 (2)	10 (9)	1 (1)	54.7 (71.9)	2.7 (3.6)	48.13 (107.64)
Light cover	91	13 (8)	21 (14)	33 (49)	20 (16)	4 (4)	36.3 (53.8)	1.8 (2.7)	15.04 (65.15)
Plains	88	2 (2)	4 (3)	11 (5)	71 (78)	0 (0)	80.7 (88.6)	4 (4.4)	202.53 (259.1)
Mountain	40	2 (1)	2 (0)	1 (0)	1 (0)	34 (39)	85 (97.5)	4.3 (4.9)	105.63 (150.16)

Table 2.7: Summary statistics for metapodial variables of extant bovids by habitat group.

(A) Complete metatarsal variables.

Variable	*N*	X	SD	OR	CI
rcMLEN				.	.
Forest	52	-0.0557	0.0657	-0.203 - 0.0374	-0.074 - -0.0374
Heavy cover	64	0.0090	0.0646	-0.149 - 0.1354	-0.0072 - 0.0251
Light cover	89	0.0281	0.0603	-0.1581 - 0.1381	0.0154 - 0.0408
Plains	94	0.0438	0.0429	-0.0902 - 0.1132	0.0351 - 0.0526
Mountain	40	-0.1076	0.0833	-0.3936 - 0.0513	-0.1342 - -0.081
cPML				.	.
Forest	52	0.0963	0.0166	0.0644 - 0.1327	0.0917 - 0.1009
Heavy cover	64	0.0831	0.0204	0.0292 - 0.1258	0.078 - 0.0882
Light cover	89	0.0810	0.0243	-0.0664 - 0.1318	0.0759 - 0.0861
Plains	94	0.0804	0.0146	0.0469 - 0.1139	0.0774 - 0.0833
Mountain	40	0.0939	0.0252	0.0568 - 0.1494	0.0858 -0.102
rcPAP				.	.
Forest	52	-0.0128	0.0326	-0.187 -0.029	-0.0218 - -0.0037
Heavy cover	64	0.0010	0.0150	-0.0373 - 0.0323	-0.0028 - 0.0047
Light cover	89	0.0058	0.0145	-0.0358 - 0.0483	0.0028 - 0.0089
Plains	94	0.0115	0.0148	-0.0245 - 0.0469	0.0084 - 0.0145
Mountain	40	-0.0249	0.0215	-0.0743 - 0.0142	-0.0317 - -0.018
rcMML				.	.
Forest	52	0.0341	0.0233	-0.021 - 0.0904	0.0277 - 0.0406
Heavy cover	64	0.0042	0.0249	-0.0472 -0.055	-0.002 - 0.0104
Light cover	89	-0.0042	0.0248	-0.0505 - 0.0612	-0.0094 -0.001
Plains	94	-0.0340	0.0276	-0.1789 - 0.0298	-0.0397 - -0.0284
Mountain	40	0.0382	0.0444	-0.0269 - 0.2173	0.024 - 0.0524
cMAP				.	.
Forest	52	-0.0892	0.0273	-0.14 - -0.029	-0.0968 - -0.0816
Heavy cover	64	-0.0907	0.0266	-0.1594 - -0.0331	-0.0973 - -0.0841
Light cover	89	-0.0872	0.0236	-0.1524 - -0.0438	-0.0921 - -0.0822
Plains	94	-0.0850	0.0246	-0.1471 - -0.0395	-0.0901 - -0.08
Mountain	40	-0.1384	0.0218	-0.1791 - -0.0893	-0.1454 - -0.1314
rcPNML				.	.
Forest	51	0.0997	0.0821	-0.1263 - 0.2303	0.0766 - 0.1228
Heavy cover	64	0.0084	0.1085	-0.2189 - 0.2119	-0.0187 - 0.0355
Light cover	89	-0.0086	0.0836	-0.2834 - 0.1995	-0.0262 -0.009
Plains	83	-0.0425	0.0817	-0.3134 - 0.1273	-0.0603 - -0.0247
Mountain	38	-0.0350	0.1167	-0.4006 - 0.1503	-0.0733 - 0.0034
cPQML				.	.
Forest	52	-0.0680	0.0235	-0.1167 - -0.0059	-0.0746 - -0.0615

Heavy cover	64	-0.1101	0.0228	-0.1666 - -0.051	-0.1158 - -0.1044
Light cover	89	-0.1259	0.0301	-0.1879 - -0.0418	-0.1323 - -0.1196
Plains	94	-0.1467	0.0372	-0.2002 - 0.0853	-0.1543 - -0.139
Mountain	40	-0.0932	0.0431	-0.1723 - 0.0797	-0.1069 - -0.0794
cPQAP				.	.
Forest	52	-0.0382	0.0362	-0.1121 - 0.0447	-0.0482 - -0.0281
Heavy cover	64	-0.0428	0.0306	-0.1157 -0.013	-0.0504 - -0.0351
Light cover	89	-0.0371	0.0235	-0.103 - 0.0255	-0.042 - -0.0321
Plains	94	-0.0282	0.0270	-0.1066 - 0.1123	-0.0338 - -0.0227
Mountain	40	-0.0974	0.0334	-0.1511 - -0.0156	-0.108 - -0.0867
rcDQML				.	.
Forest	52	0.0463	0.0408	-0.0376 -0.146	0.0349 - 0.0577
Heavy cover	64	0.0112	0.0386	-0.0714 - 0.0882	0.0016 - 0.0209
Light cover	89	-0.0147	0.0347	-0.0947 - 0.0858	-0.022 - -0.0074
Plains	94	-0.0433	0.0348	-0.13 - 0.0389	-0.0505 - -0.0362
Mountain	40	0.0564	0.0663	-0.061 - 0.2197	0.0352 - 0.0776
rcDQAP				.	.
Forest	52	0.0288	0.0200	-0.0364 - 0.0694	0.0232 - 0.0344
Heavy cover	64	0.0093	0.0228	-0.0685 - 0.0539	0.0036 -0.015
Light cover	89	0.0002	0.0241	-0.0527 - 0.0762	-0.0049 - 0.0052
Plains	94	-0.0142	0.0220	-0.063 - 0.0307	-0.0187 - -0.0097
Mountain	40	-0.0193	0.0312	-0.0901 - 0.0547	-0.0293 - -0.0094
rcEMAP				.	.
Forest	52	-0.0049	0.0206	-0.0543 - 0.0369	-0.0107 - 0.0008
Heavy cover	64	0.0085	0.0282	-0.0361 - 0.0688	0.0015 - 0.0155
Light cover	89	0.0077	0.0243	-0.0571 - 0.0682	0.0026 - 0.0128
Plains	94	0.0077	0.0186	-0.0561 - 0.0402	0.0039 - 0.0115
Mountain	40	-0.0424	0.0374	-0.1005 - 0.0415	-0.0544 - -0.0304
rcMVAP				.	.
Forest	52	-0.0196	0.0150	-0.0439 -0.016	-0.0238 - -0.0154
Heavy cover	64	-0.0003	0.0171	-0.0366 - 0.0383	-0.0045 -0.004
Light cover	89	0.0048	0.0136	-0.0349 - 0.0311	0.002 - 0.0077
Plains	94	0.0062	0.0109	-0.0321 - 0.0297	0.004 - 0.0084
Mountain	40	0.0006	0.0233	-0.0914 - 0.0381	-0.0069 -0.008
rcIMAP				.	.
Forest	52	-0.0084	0.0156	-0.0433 - 0.0333	-0.0127 - -0.0041
Heavy cover	64	0.0025	0.0202	-0.0364 - 0.0439	-0.0026 - 0.0075
Light cover	89	0.0035	0.0157	-0.0266 - 0.0391	0.0002 - 0.0068
Plains	94	0.0052	0.0129	-0.0302 - 0.0382	0.0026 - 0.0078
Mountain	40	-0.0131	0.0173	-0.0632 - 0.0208	-0.0186 - -0.0076
rcELAP				.	.
Forest	52	-0.0146	0.0260	-0.0694 - 0.0451	-0.0218 - -0.0074
Heavy cover	64	0.0113	0.0379	-0.0813 - 0.0887	0.0018 - 0.0207
Light cover	89	0.0078	0.0275	-0.0727 - 0.0643	0.002 - 0.0136
Plains	94	0.0065	0.0213	-0.0462 - 0.0485	0.0022 - 0.0109

Mountain	40	-0.0318	0.0346	-0.0906 - 0.0456	-0.0429 - -0.0207
rcLVAP				.	.
Forest	52	-0.0160	0.0203	-0.0584 -0.025	-0.0217 - -0.0103
Heavy cover	64	0.0019	0.0178	-0.0365 - 0.0481	-0.0025 - 0.0064
Light cover	89	0.0042	0.0137	-0.0377 - 0.0295	0.0013 - 0.0071
Plains	94	0.0034	0.0121	-0.0347 - 0.0328	0.0009 - 0.0059
Mountain	40	0.0003	0.0215	-0.0801 - 0.0356	-0.0065 - 0.0072
rcILAP				.	.
Forest	52	0.0003	0.0186	-0.0475 - 0.0421	-0.0049 - 0.0054
Heavy cover	64	0.0045	0.0168	-0.0298 - 0.0384	0.0003 - 0.0087
Light cover	89	0.0028	0.0141	-0.0284 - 0.0365	-0.0001 - 0.0058
Plains	94	0.0015	0.0128	-0.0317 - 0.0339	-0.0011 - 0.0042
Mountain	40	-0.0175	0.0168	-0.0653 -0.011	-0.0229 - -0.0121
rcAVML				.	.
Forest	52	-0.0166	0.0356	-0.0874 - 0.0573	-0.0265 - -0.0067
Heavy cover	64	-0.0179	0.0525	-0.1403 - 0.0726	-0.031 - -0.0048
Light cover	89	-0.0077	0.0370	-0.091 - 0.0612	-0.0155 - 0.0001
Plains	94	0.0062	0.0289	-0.0554 -0.073	0.0003 - 0.0121
Mountain	40	0.0527	0.0386	-0.0041 - 0.1507	0.0403 -0.065
rcIVML				.	.
Forest	52	-0.0257	0.0385	-0.0882 - 0.0592	-0.0365 - -0.015
Heavy cover	64	-0.0200	0.0488	-0.1313 -0.057	-0.0321 - -0.0078
Light cover	89	-0.0093	0.0293	-0.0925 - 0.0431	-0.0155 - -0.0032
Plains	94	0.0154	0.0239	-0.032 - 0.0659	0.0105 - 0.0203
Mountain	40	0.0499	0.0291	-0.0127 - 0.1149	0.0405 - 0.0592
rcPVML				.	.
Forest	52	-0.0138	0.0280	-0.0637 - 0.0455	-0.0215 - -0.006
Heavy cover	64	-0.0152	0.0429	-0.1009 - 0.0706	-0.0259 - -0.0044
Light cover	89	-0.0071	0.0260	-0.0901 - 0.0392	-0.0126 - -0.0016
Plains	94	0.0065	0.0172	-0.0208 - 0.0612	0.003 - 0.0101
Mountain	40	0.0426	0.0348	-0.0433 - 0.0986	0.0315 - 0.0537
rcADML				.	.
Forest	52	-0.0201	0.0346	-0.0961 - 0.06	-0.0297 - -0.0104
Heavy cover	64	-0.0196	0.0425	-0.1354 - 0.0899	-0.0302 - -0.009
Light cover	89	-0.0056	0.0291	-0.0653 - 0.0443	-0.0118 - 0.0005
Plains	94	0.0120	0.0207	-0.0414 - 0.0886	0.0078 - 0.0163
Mountain	40	0.0417	0.0313	-0.0193 - 0.0978	0.0317 - 0.0518
rcIDML				.	.
Forest	52	-0.0184	0.0347	-0.0868 - 0.0565	-0.0281 - -0.0088
Heavy cover	64	-0.0155	0.0351	-0.0941 -0.056	-0.0243 - -0.0067
Light cover	89	-0.0080	0.0233	-0.0519 -0.029	-0.0129 - -0.0031
Plains	94	0.0089	0.0190	-0.0292 - 0.0608	0.0051 - 0.0128
Mountain	40	0.0457	0.0240	0.0011 -0.087	0.038 - 0.0534
rcPDML				.	.
Forest	52	-0.0086	0.0309	-0.0636 - 0.0551	-0.0171 -0

Heavy cover	64	-0.0120	0.0299	-0.0746 - 0.0568	-0.0194 - -0.0045
Light cover	88	-0.0091	0.0238	-0.0714 - 0.0342	-0.0142 - -0.0041
Plains	94	0.0013	0.0185	-0.0315 - 0.0504	-0.0025 -0.005
Mountain	40	0.0474	0.0256	0.0014 - 0.0988	0.0392 - 0.0556
rcDDML				.	.
Forest	52	0.0041	0.0204	-0.0361 - 0.0489	-0.0015 - 0.0098
Heavy cover	64	-0.0045	0.0212	-0.0534 - 0.0434	-0.0098 - 0.0008
Light cover	89	-0.0110	0.0196	-0.0714 - 0.0282	-0.0151 - -0.0069
Plains	94	-0.0044	0.0150	-0.0356 -0.035	-0.0074 - -0.0013
Mountain	40	0.0366	0.0202	-0.0034 -0.076	0.0301 - 0.0431
rcDDAP				.	.
Forest	52	0.0102	0.0258	-0.0455 - 0.0532	0.003 - 0.0174
Heavy cover	64	0.0209	0.0224	-0.0214 - 0.0666	0.0154 - 0.0265
Light cover	89	0.0101	0.0364	-0.0695 - 0.1739	0.0024 - 0.0178
Plains	94	-0.0164	0.0262	-0.0806 - 0.0457	-0.0218 - -0.011
Mountain	40	-0.0307	0.0342	-0.1054 - 0.0351	-0.0416 - -0.0198
rcDEML				.	.
Forest	52	-0.0048	0.0284	-0.0751 - 0.0453	-0.0127 - 0.0031
Heavy cover	64	-0.0084	0.0273	-0.0747 - 0.0521	-0.0152 - -0.0016
Light cover	88	-0.0091	0.0320	-0.209 - 0.0517	-0.0158 - -0.0023
Plains	94	-0.0002	0.0176	-0.0313 - 0.0417	-0.0038 - 0.0034
Mountain	40	0.0400	0.0236	0.0053 - 0.0842	0.0325 - 0.0476
cDEAP				.	.
Forest	52	-0.1233	0.0577	-0.2262 - -0.0379	-0.1394 - -0.1073
Heavy cover	64	-0.1115	0.0452	-0.2224 - -0.0359	-0.1228 - -0.1002
Light cover	89	-0.1105	0.0490	-0.2088 - 0.1052	-0.1209 - -0.1002
Plains	94	-0.1157	0.0274	-0.1878 - -0.0564	-0.1213 - -0.11
Mountain	40	-0.1212	0.0214	-0.1769 - -0.0808	-0.1281 - -0.1144
rcIIML				.	.
Forest	52	-0.0287	0.0807	-0.2193 -0.131	-0.0511 - -0.0062
Heavy cover	64	-0.0293	0.0984	-0.2743 - 0.2118	-0.0539 - -0.0048
Light cover	89	-0.0285	0.0697	-0.175 - 0.1454	-0.0432 - -0.0138
Plains	94	0.0258	0.0521	-0.0913 - 0.1557	0.0151 - 0.0364
Mountain	40	0.0871	0.0616	-0.033 - 0.2205	0.0674 - 0.1068

Key: *N*, sample size; X, mean; SD, standard deviation; OR, observed range; CI; 95% confidence intervals.

Table 2.7: Summary statistics for metapodial variables of extant bovids by habitat group.

(B) Complete metacarpal variables.

Variable	*N*	X	SD	OR	CI
rcMLEN				.	.
Forest	53	-0.0710	0.0866	-0.2598 - 0.0517	-0.0948 - -0.0471
Heavy cover	64	0.0167	0.0778	-0.1786 - 0.1547	-0.0027 - 0.0361
Light cover	91	0.0413	0.0811	-0.1841 - 0.2214	0.0244 - 0.0582
Plains	88	0.0465	0.0605	-0.1403 -0.124	0.0336 - 0.0593
Mountain	40	-0.1287	0.0956	-0.4608 - 0.0475	-0.1593 - -0.0982
rcPML				.	.
Forest	53	-0.0011	0.0466	-0.2116 - 0.0602	-0.014 - 0.0117
Heavy cover	64	-0.0002	0.0304	-0.176 - 0.0585	-0.0078 - 0.0074
Light cover	91	-0.0001	0.0220	-0.0434 - 0.0623	-0.0046 - 0.0045
Plains	88	-0.0015	0.0212	-0.0819 - 0.0457	-0.006 -0.003
Mountain	40	0.0053	0.0277	-0.1091 - 0.0618	-0.0036 - 0.0141
rcPAP				.	.
Forest	53	0.0055	0.0453	-0.0734 - 0.22	-0.007 -0.018
Heavy cover	64	-0.0009	0.0274	-0.0412 - 0.1697	-0.0077 - 0.0059
Light cover	91	0.0024	0.0143	-0.0381 - 0.0326	-0.0006 - 0.0054
Plains	88	-0.0017	0.0141	-0.0352 - 0.0389	-0.0047 - 0.0013
Mountain	40	-0.0075	0.0262	-0.0561 - 0.0814	-0.0159 - 0.0008
rcMML				.	.
Forest	53	0.0280	0.0309	-0.0276 - 0.1044	0.0194 - 0.0365
Heavy cover	64	-0.0036	0.0279	-0.0494 - 0.0708	-0.0106 - 0.0033
Light cover	91	-0.0059	0.0298	-0.0749 - 0.0938	-0.0121 - 0.0003
Plains	88	-0.0327	0.0247	-0.0843 - 0.0567	-0.038 - -0.0275
Mountain	40	0.0542	0.0458	-0.0372 - 0.1988	0.0396 - 0.0689
rcMAP				.	.
Forest	53	0.0049	0.0306	-0.0601 -0.105	-0.0035 - 0.0133
Heavy cover	64	0.0061	0.0364	-0.0699 - 0.1404	-0.003 - 0.0152
Light cover	91	0.0101	0.0278	-0.0681 - 0.0654	0.0043 - 0.0159
Plains	88	-0.0023	0.0203	-0.0478 - 0.0466	-0.0066 -0.002
Mountain	40	-0.0341	0.0393	-0.1055 - 0.1157	-0.0467 - -0.0216
cMGML				.	.
Forest	53	-0.0459	0.0369	-0.1442 - 0.0482	-0.0561 - -0.0357
Heavy cover	64	-0.0377	0.0283	-0.1024 - 0.0096	-0.0448 - -0.0306
Light cover	91	-0.0246	0.0234	-0.0832 - 0.0345	-0.0295 - -0.0197
Plains	88	-0.0066	0.0298	-0.1325 - 0.0484	-0.013 - -0.0003
Mountain	40	-0.0464	0.0628	-0.3738 - 0.0184	-0.0664 - -0.0263
rcPQML				.	.
Forest	53	0.0334	0.0300	-0.0116 - 0.1078	0.0252 - 0.0417

Heavy cover	64	0.0023	0.0340	-0.0586 - 0.0804	-0.0062 - 0.0108
Light cover	91	-0.0079	0.0336	-0.078 - 0.0942	-0.0149 - -0.0008
Plains	88	-0.0333	0.0301	-0.0863 -0.089	-0.0397 - -0.0269
Mountain	40	0.0431	0.0432	-0.0515 - 0.1899	0.0293 - 0.0569
cPQAP				.	.
Forest	53	-0.1129	0.0307	-0.1693 - -0.0175	-0.1214 - -0.1045
Heavy cover	64	-0.1198	0.0334	-0.184 - -0.0588	-0.1281 - -0.1115
Light cover	91	-0.1132	0.0267	-0.2073 - -0.0625	-0.1188 - -0.1076
Plains	88	-0.1264	0.0236	-0.1981 - -0.0566	-0.1314 - -0.1214
Mountain	40	-0.1626	0.0393	-0.2439 - -0.0671	-0.1752 - -0.15
rcDQML				.	.
Forest	53	0.0372	0.0501	-0.0643 - 0.1549	0.0234 -0.051
Heavy cover	64	-0.0037	0.0475	-0.0919 - 0.0974	-0.0156 - 0.0081
Light cover	91	-0.0176	0.0449	-0.1195 - 0.15	-0.0269 - -0.0083
Plains	88	-0.0342	0.0421	-0.1283 - 0.1205	-0.0431 - -0.0253
Mountain	40	0.0719	0.0637	-0.0678 - 0.2019	0.0516 - 0.0923
cDQAP				.	.
Forest	53	-0.1644	0.0307	-0.2406 - -0.0994	-0.1729 - -0.156
Heavy cover	64	-0.1719	0.0319	-0.284 - -0.109	-0.1799 - -0.1639
Light cover	91	-0.1804	0.0478	-0.235 - 0.2095	-0.1904 - -0.1705
Plains	88	-0.1956	0.0313	-0.2962 - -0.0446	-0.2022 - -0.189
Mountain	40	-0.1883	0.0295	-0.2336 - -0.1167	-0.1978 - -0.1789
rcEMAP				.	.
Forest	53	-0.0080	0.0283	-0.0581 - 0.0432	-0.0158 - -0.0002
Heavy cover	64	0.0068	0.0344	-0.0433 - 0.0757	-0.0018 - 0.0154
Light cover	91	0.0075	0.0256	-0.0604 - 0.0622	0.0022 - 0.0129
Plains	88	0.0205	0.0211	-0.0328 - 0.0608	0.016 -0.025
Mountain	40	-0.0626	0.0389	-0.1341 - 0.0026	-0.075 - -0.0501
cMVAP				.	.
Forest	53	-0.0254	0.0216	-0.0804 - 0.0141	-0.0314 - -0.0195
Heavy cover	64	-0.0123	0.0271	-0.0724 - 0.0348	-0.019 - -0.0055
Light cover	91	-0.0094	0.0246	-0.0741 -0.096	-0.0146 - -0.0043
Plains	88	-0.0033	0.0205	-0.0674 - 0.0301	-0.0076 - 0.0011
Mountain	40	-0.0245	0.0249	-0.0977 - 0.0151	-0.0325 - -0.0166
rcIMAP				.	.
Forest	53	-0.0072	0.0209	-0.0586 - 0.0417	-0.013 - -0.0015
Heavy cover	64	0.0041	0.0252	-0.0463 -0.058	-0.0022 - 0.0104
Light cover	91	0.0042	0.0191	-0.0505 - 0.0387	0.0002 - 0.0081
Plains	88	0.0104	0.0165	-0.0299 - 0.0415	0.0069 - 0.0139
Mountain	40	-0.0294	0.0192	-0.0666 - 0.0105	-0.0355 - -0.0232
rcELAP				.	.
Forest	53	-0.0083	0.0362	-0.0888 - 0.0547	-0.0182 - 0.0017
Heavy cover	64	0.0094	0.0415	-0.0584 - 0.1024	-0.001 - 0.0198
Light cover	91	0.0118	0.0306	-0.0858 - 0.0637	0.0055 - 0.0182
Plains	88	0.0176	0.0256	-0.0502 - 0.0654	0.0122 - 0.0231

Mountain	40	-0.0698	0.0376	-0.1382 - 0.0046	-0.0818 - -0.0578
rcLVAP				.	.
Forest	53	-0.0175	0.0237	-0.0635 - 0.0286	-0.024 - -0.0109
Heavy cover	64	0.0052	0.0240	-0.0382 - 0.0668	-0.0008 - 0.0112
Light cover	91	0.0045	0.0183	-0.0427 - 0.0382	0.0007 - 0.0083
Plains	88	0.0091	0.0170	-0.0436 - 0.0494	0.0054 - 0.0127
Mountain	40	-0.0155	0.0211	-0.0849 - 0.0229	-0.0222 - -0.0087
rcILAP				.	.
Forest	53	-0.0094	0.0214	-0.0601 - 0.0286	-0.0153 - -0.0035
Heavy cover	64	0.0062	0.0238	-0.0338 - 0.0567	0.0002 - 0.0121
Light cover	91	0.0067	0.0181	-0.0421 - 0.0409	0.0029 - 0.0104
Plains	88	0.0106	0.0171	-0.0312 - 0.0505	0.0069 - 0.0142
Mountain	40	-0.0357	0.0199	-0.0805 - 0.0107	-0.0421 - -0.0294
rcAVML				.	.
Forest	53	-0.0188	0.0317	-0.0828 - 0.0417	-0.0276 - -0.0101
Heavy cover	64	-0.0210	0.0465	-0.1364 - 0.0724	-0.0326 - -0.0093
Light cover	91	-0.0127	0.0284	-0.0854 - 0.0444	-0.0186 - -0.0068
Plains	88	0.0092	0.0284	-0.0616 - 0.0917	0.0032 - 0.0152
Mountain	40	0.0671	0.0365	-0.0018 - 0.1473	0.0554 - 0.0788
rcIVML				.	.
Forest	53	-0.0216	0.0395	-0.1151 - 0.0516	-0.0324 - -0.0107
Heavy cover	64	-0.0201	0.0441	-0.1063 - 0.0575	-0.0311 - -0.0091
Light cover	91	-0.0108	0.0284	-0.0813 - 0.0534	-0.0167 - -0.0048
Plains	88	0.0140	0.0300	-0.0451 - 0.0839	0.0077 - 0.0204
Mountain	40	0.0543	0.0357	-0.0164 - 0.1103	0.0429 - 0.0657
rcPVML				.	.
Forest	53	-0.0106	0.0327	-0.0707 - 0.0519	-0.0196 - -0.0015
Heavy cover	64	-0.0126	0.0375	-0.0849 - 0.0663	-0.0219 - -0.0032
Light cover	91	-0.0092	0.0287	-0.0814 - 0.0691	-0.0152 - -0.0032
Plains	88	0.0030	0.0233	-0.051 - 0.0574	-0.0019 - 0.0079
Mountain	40	0.0484	0.0301	-0.0201 - 0.0963	0.0388 - 0.0581
rcADML				.	.
Forest	53	-0.0190	0.0390	-0.0954 - 0.0787	-0.0297 - -0.0082
Heavy cover	64	-0.0164	0.0415	-0.1032 -0.055	-0.0267 - -0.006
Light cover	91	-0.0105	0.0342	-0.1432 - 0.0726	-0.0176 - -0.0033
Plains	88	0.0108	0.0248	-0.0468 - 0.0662	0.0055 -0.016
Mountain	40	0.0514	0.0296	-0.0064 - 0.1152	0.0419 - 0.0609
rcIDML				.	.
Forest	53	-0.0083	0.0358	-0.0807 -0.061	-0.0181 - 0.0016
Heavy cover	64	-0.0116	0.0356	-0.0853 - 0.0679	-0.0205 - -0.0027
Light cover	91	-0.0123	0.0251	-0.0724 - 0.0444	-0.0176 - -0.0071
Plains	88	0.0039	0.0248	-0.0459 - 0.0625	-0.0014 - 0.0091
Mountain	40	0.0490	0.0240	0.0024 - 0.0853	0.0414 - 0.0567
rcPDML				.	.
Forest	53	0.0035	0.0348	-0.063 - 0.0735	-0.0061 - 0.0131

Heavy cover	64	-0.0112	0.0338	-0.0815 - 0.0776	-0.0196 - -0.0027
Light cover	91	-0.0113	0.0269	-0.0979 - 0.0458	-0.0169 - -0.0057
Plains	88	-0.0049	0.0263	-0.0608 - 0.0537	-0.0105 - 0.0006
Mountain	40	0.0497	0.0269	-0.0082 - 0.0902	0.0411 - 0.0583
rcDDML				.	.
Forest	53	0.0056	0.0235	-0.0532 - 0.0633	-0.0008 - 0.0121
Heavy cover	64	-0.0061	0.0221	-0.0546 - 0.0457	-0.0116 - -0.0006
Light cover	91	-0.0121	0.0195	-0.0588 - 0.0455	-0.0161 - -0.008
Plains	88	-0.0072	0.0160	-0.0462 - 0.0281	-0.0106 - -0.0038
Mountain	40	0.0456	0.0204	0.0079 - 0.0889	0.0391 - 0.0521
rcDDAP				.	.
Forest	53	0.0125	0.0394	-0.0825 - 0.0947	0.0016 - 0.0233
Heavy cover	64	0.0260	0.0364	-0.0458 - 0.0907	0.0169 - 0.0351
Light cover	91	0.0024	0.0267	-0.0593 - 0.0616	-0.0031 -0.008
Plains	88	-0.0179	0.0258	-0.0707 - 0.0589	-0.0233 - -0.0124
Mountain	40	-0.0243	0.0260	-0.0851 - 0.0551	-0.0326 - -0.016
rcDEML				.	.
Forest	53	0.0089	0.0320	-0.0524 - 0.0659	0.0001 - 0.0177
Heavy cover	64	-0.0063	0.0288	-0.0827 -0.058	-0.0135 - 0.0009
Light cover	91	-0.0094	0.0281	-0.0879 - 0.0442	-0.0153 - -0.0036
Plains	88	-0.0079	0.0258	-0.1086 - 0.0374	-0.0133 - -0.0024
Mountain	40	0.0370	0.0255	-0.0142 - 0.0878	0.0289 - 0.0452
cDEAP				.	.
Forest	53	-0.1106	0.0460	-0.1974 - -0.0191	-0.1233 - -0.0979
Heavy cover	64	-0.1030	0.0421	-0.1967 - -0.0007	-0.1135 - -0.0924
Light cover	91	-0.1080	0.0303	-0.1884 - -0.0422	-0.1143 - -0.1016
Plains	88	-0.1089	0.0221	-0.1527 - -0.0556	-0.1136 - -0.1042
Mountain	40	-0.1343	0.0287	-0.1884 - -0.0696	-0.1435 - -0.1251
rcIIML				.	.
Forest	53	-0.0047	0.0880	-0.1985 - 0.1533	-0.029 - 0.0196
Heavy cover	64	-0.0457	0.1053	-0.299 - 0.1517	-0.072 - -0.0194
Light cover	91	-0.0365	0.0699	-0.2023 - 0.1319	-0.051 - -0.0219
Plains	88	0.0179	0.0686	-0.1858 - 0.2124	0.0034 - 0.0324
Mountain	40	0.1229	0.0882	-0.0649 - 0.3019	0.0947 - 0.1511

Key: *N*, sample size; X, mean; SD, standard deviation; OR, observed range; CI; 95% confidence intervals.

Table 2.7: Summary statistics for metapodial variables of extant bovids by habitat group.

(C) Distal metatarsal variables.

Variable	*N*	X	SD	OR	CI
rINFANT				.	.
Forest	52	-0.0075	0.0347	-0.0832 - 0.0727	-0.0171 - 0.0022
Heavy cover	64	-0.0010	0.0306	-0.0543 - 0.0706	-0.0087 - 0.0066
Light cover	90	-0.0005	0.0289	-0.1401 - 0.0596	-0.0065 - 0.0056
Plains	94	0.0100	0.0172	-0.0262 - 0.0485	0.0065 - 0.0135
Mountain	40	-0.0018	0.0380	-0.0676 - 0.0757	-0.0139 - 0.0104
POSANT				.	.
Forest	52	0.0652	0.0264	0.0012 - 0.1247	0.0579 - 0.0726
Heavy cover	64	0.0652	0.0349	-0.0067 - 0.1624	0.0565 - 0.0739
Light cover	90	0.0630	0.0310	0.0011 - 0.1268	0.0565 - 0.0695
Plains	94	0.0629	0.0217	0.0087 - 0.1158	0.0584 - 0.0673
Mountain	40	0.0524	0.0451	-0.0671 - 0.1312	0.0379 - 0.0668
rPOSINF				.	.
Forest	52	0.0113	0.0233	-0.0349 - 0.0723	0.0048 - 0.0178
Heavy cover	64	0.0046	0.0197	-0.0302 - 0.0437	-0.0004 - 0.0095
Light cover	90	0.0019	0.0214	-0.0346 - 0.1169	-0.0026 - 0.0063
Plains	94	-0.0089	0.0161	-0.0483 - 0.0262	-0.0122 - -0.0056
Mountain	40	-0.0074	0.0198	-0.0791 - 0.0267	-0.0137 - -0.001
rdEMAP				.	.
Forest	52	0.0026	0.0205	-0.0422 - 0.0378	-0.0031 - 0.0083
Heavy cover	64	0.0101	0.0268	-0.0351 - 0.0684	0.0034 - 0.0168
Light cover	90	0.0090	0.0230	-0.0489 - 0.0605	0.0041 - 0.0138
Plains	94	0.0045	0.0168	-0.0507 - 0.0353	0.001 - 0.0079
Mountain	40	-0.0464	0.0317	-0.0949 - 0.0247	-0.0566 - -0.0363
rdMVAP				.	.
Forest	52	-0.0126	0.0139	-0.0427 - 0.0158	-0.0165 - -0.0088
Heavy cover	64	0.0009	0.0153	-0.0295 - 0.0402	-0.003 - 0.0047
Light cover	90	0.0053	0.0124	-0.027 - 0.0322	0.0027 - 0.0079
Plains	94	0.0027	0.0093	-0.0272 - 0.0227	0.0008 - 0.0046
Mountain	40	-0.0036	0.0164	-0.0569 - 0.0247	-0.0088 - 0.0016
rdIMAP				.	.
Forest	52	-0.0014	0.0147	-0.0407 - 0.0381	-0.0055 - 0.0027
Heavy cover	64	0.0038	0.0191	-0.0277 - 0.0463	-0.001 - 0.0086
Light cover	90	0.0043	0.0151	-0.0239 - 0.0391	0.0012 - 0.0075
Plains	94	0.0019	0.0110	-0.0303 - 0.0239	-0.0004 - 0.0041
Mountain	40	-0.0171	0.0134	-0.0547 - 0.0079	-0.0214 - -0.0128
rdELAP				.	.
Forest	52	-0.0072	0.0258	-0.0675 - 0.0442	-0.0144 -0

Heavy cover	64	0.0129	0.0380	-0.0894 - 0.0918	0.0034 - 0.0224
Light cover	90	0.0088	0.0270	-0.0693 - 0.0642	0.0032 - 0.0145
Plains	94	0.0035	0.0199	-0.047 - 0.0447	-0.0006 - 0.0076
Mountain	40	-0.0354	0.0293	-0.0885 - 0.0312	-0.0448 - -0.026
rdLVAP				.	.
Forest	52	-0.0092	0.0193	-0.058 - 0.0199	-0.0146 - -0.0039
Heavy cover	64	0.0030	0.0175	-0.0451 - 0.0509	-0.0014 - 0.0074
Light cover	90	0.0046	0.0131	-0.0317 - 0.0367	0.0018 - 0.0073
Plains	94	-0.0001	0.0101	-0.0299 - 0.0191	-0.0022 - 0.0019
Mountain	40	-0.0039	0.0147	-0.0462 - 0.0204	-0.0086 - 0.0008
rdILAP				.	.
Forest	52	0.0072	0.0177	-0.0375 - 0.0397	0.0023 - 0.0121
Heavy cover	64	0.0057	0.0162	-0.0266 - 0.0403	0.0016 - 0.0097
Light cover	90	0.0035	0.0140	-0.025 - 0.0359	0.0006 - 0.0065
Plains	94	-0.0020	0.0105	-0.0325 - 0.02	-0.0042 - 0.0002
Mountain	40	-0.0219	0.0135	-0.0554 - -0.0007	-0.0262 - -0.0176
rdAVML				.	.
Forest	52	-0.0105	0.0339	-0.082 - 0.0568	-0.0199 - -0.0011
Heavy cover	64	-0.0179	0.0528	-0.1366 - 0.0642	-0.0311 - -0.0047
Light cover	90	-0.0083	0.0360	-0.0914 - 0.0607	-0.0158 - -0.0007
Plains	94	0.0010	0.0285	-0.0633 - 0.0631	-0.0048 - 0.0069
Mountain	40	0.0465	0.0429	-0.0244 - 0.1516	0.0328 - 0.0602
rdIVML				.	.
Forest	52	-0.0180	0.0376	-0.0784 - 0.0618	-0.0284 - -0.0075
Heavy cover	64	-0.0190	0.0476	-0.1274 -0.053	-0.0308 - -0.0071
Light cover	90	-0.0087	0.0280	-0.0937 - 0.0395	-0.0146 - -0.0029
Plains	94	0.0110	0.0235	-0.0376 - 0.0712	0.0062 - 0.0159
Mountain	40	0.0447	0.0300	-0.0202 - 0.1027	0.0351 - 0.0543
rdPVML				.	.
Forest	52	-0.0067	0.0272	-0.0645 - 0.0489	-0.0143 - 0.0009
Heavy cover	64	-0.0144	0.0426	-0.0985 - 0.0607	-0.0251 - -0.0038
Light cover	90	-0.0069	0.0251	-0.0898 - 0.0375	-0.0121 - -0.0016
Plains	94	0.0022	0.0174	-0.0306 - 0.0531	-0.0014 - 0.0057
Mountain	40	0.0373	0.0338	-0.0492 - 0.0873	0.0265 - 0.0482
rdADML				.	.
Forest	52	-0.0133	0.0332	-0.0747 - 0.0614	-0.0225 - -0.004
Heavy cover	64	-0.0191	0.0424	-0.1444 - 0.0799	-0.0297 - -0.0085
Light cover	90	-0.0056	0.0286	-0.0683 - 0.0478	-0.0116 - 0.0004
Plains	94	0.0074	0.0214	-0.0438 - 0.0854	0.003 - 0.0118
Mountain	40	0.0361	0.0373	-0.0311 - 0.1353	0.0242 -0.048
rdIDML				.	.
Forest	52	-0.0105	0.0330	-0.0637 -0.057	-0.0197 - -0.0013
Heavy cover	64	-0.0143	0.0341	-0.092 - 0.0459	-0.0228 - -0.0057
Light cover	90	-0.0072	0.0220	-0.0572 - 0.0352	-0.0118 - -0.0026
Plains	94	0.0048	0.0186	-0.0327 - 0.0655	0.001 - 0.0086

Mountain	40	0.0407	0.0278	-0.01 - 0.0832	0.0318 - 0.0496
rdPDML				.	.
Forest	52	-0.0012	0.0297	-0.0477 - 0.0555	-0.0094 - 0.0071
Heavy cover	64	-0.0110	0.0292	-0.0728 - 0.0469	-0.0183 - -0.0038
Light cover	90	-0.0083	0.0238	-0.0722 - 0.0409	-0.0133 - -0.0033
Plains	94	-0.0031	0.0184	-0.0343 - 0.0534	-0.0069 - 0.0007
Mountain	40	0.0421	0.0273	-0.0065 - 0.0962	0.0333 - 0.0508
rdDDML				.	.
Forest	52	0.0116	0.0192	-0.0331 -0.051	0.0063 - 0.0169
Heavy cover	64	-0.0034	0.0208	-0.0473 - 0.0339	-0.0086 - 0.0018
Light cover	90	-0.0103	0.0192	-0.0632 - 0.0326	-0.0143 - -0.0062
Plains	94	-0.0085	0.0159	-0.0374 - 0.0404	-0.0118 - -0.0053
Mountain	40	0.0314	0.0236	-0.0225 - 0.0727	0.0239 - 0.0389
rdDDAP				.	.
Forest	52	0.0165	0.0271	-0.0447 - 0.0586	0.009 - 0.0241
Heavy cover	64	0.0217	0.0222	-0.0276 - 0.0665	0.0162 - 0.0273
Light cover	90	0.0105	0.0374	-0.078 -0.181	0.0027 - 0.0184
Plains	94	-0.0203	0.0273	-0.0951 - 0.0448	-0.0259 - -0.0147
Mountain	40	-0.0358	0.0321	-0.1108 - 0.0173	-0.0461 - -0.0255
rdDEML				.	.
Forest	52	0.0028	0.0280	-0.0721 - 0.0467	-0.005 - 0.0106
Heavy cover	64	-0.0073	0.0267	-0.0686 - 0.0422	-0.014 - -0.0007
Light cover	90	-0.0084	0.0312	-0.2073 - 0.0338	-0.015 - -0.0018
Plains	94	-0.0045	0.0190	-0.037 - 0.0471	-0.0084 - -0.0007
Mountain	40	0.0346	0.0267	-0.0087 - 0.0838	0.0261 - 0.0432
dDEAP				.	.
Forest	52	-0.1228	0.0559	-0.2248 - -0.0378	-0.1383 - -0.1072
Heavy cover	64	-0.1169	0.0439	-0.2167 - -0.0376	-0.1278 - -0.1059
Light cover	90	-0.1159	0.0494	-0.2155 - 0.1002	-0.1262 - -0.1055
Plains	94	-0.1259	0.0268	-0.1943 - -0.0734	-0.1314 - -0.1205
Mountain	40	-0.1325	0.0194	-0.1778 - -0.0981	-0.1387 - -0.1263
rdIIML				.	.
Forest	52	-0.0162	0.0807	-0.2039 - 0.1426	-0.0386 - 0.0063
Heavy cover	64	-0.0245	0.0998	-0.275 - 0.2248	-0.0494 - 0.0004
Light cover	90	-0.0249	0.0670	-0.1746 - 0.1303	-0.0389 - -0.0109
Plains	94	0.0257	0.0519	-0.0912 - 0.1562	0.0151 - 0.0363
Mountain	40	0.0879	0.0631	-0.038 - 0.2171	0.0677 - 0.1081

Key: *N*, sample size; X, mean; SD, standard deviation; OR, observed range; CI; 95% confidence intervals.

Table 2.8: Morphology and habitat relationship by three criteria.

(A) Complete metatarsal variables.

Variable	Trend	Group Distinguished	Means Compared	*df*	χ^2	*P*
rcMLEN	increases from forest to plains	Forest, Mountain	less than	1	64.68	<.05
cPML	decreases from forest to plains		greater than	1	27.02	<.05
rcPAP	increases from forest to plains		less than	1	34.39	<.05
rcMML	decreases from forest to plains	Plains	greater than	1	89.73	<.05
cMAP	no monotonic trend	Mountain	less than	1	1.92	0.17
rcPNML	decreases from forest to plains	Forest	greater than	1	57.90	<.05
cPQML	decreases from forest to plains	Forest, Light cover, Plains	greater than	1	86.28	<.05
cPQAP	no monotonic trend	Mountain	less than	1	4.29	<.05
rcDQML	decreases from forest to plains	Heavy cover, Light cover, Plains	greater than	1	82.75	<.05
rcDQAP	decreases from forest to plains	Forest	greater than	1	74.71	<.05
rcEMAP	no monotonic trend	Forest, Mountain	less than	1	13.77	<.05
rcMVAP	increases from forest to plains	Forest	less than	1	67.34	<.05
rcIMAP	increases from forest to plains		less than	1	26.56	<.05
rcELAP	no monotonic trend		less than	1	22.82	<.05
rcLVAP	no monotonic trend	Forest	less than	1	33.58	<.05
rcILAP	no monotonic trend	Mountain	less than	1	0.08	0.77
rcAVML	no monotonic trend	Plains, Mountain	less than	1	12.67	<.05
rcIVML	increases from forest to plains	Plains, Mountain	less than	1	41.96	<.05
rcPVML	no monotonic trend	Plains, Mountain	less than	1	21.10	<.05
rcADML	increases from forest to plains	Plains, Mountain	less than	1	31.39	<.05
rcIDML	increases from forest to plains	Plains, Mountain	less than	1	27.41	<.05
rcPDML	no monotonic trend	Mountain	less than	1	5.07	<.05
rcDDML	no monotonic trend	Mountain	greater than	1	7.70	<.05
rcDDAP	no monotonic trend		greater than	1	26.22	<.05
rcDEML	no monotonic trend	Mountain	less than	1	0.60	0.44
cDEAP	no monotonic trend		less than	1	0.13	0.72
rcIIML	no monotonic trend	Plains, Mountain	less than	1	17.24	<.05

Table 2.8: Morphology and habitat relationship by three criteria.

(B) Complete metacarpal variables.

Variable	Trend	Group Distinguished	Means Compared	*df*	χ^2	*P*
rcMLEN	increases from forest to plains	Forest, Mountain	less than	1	57.41	<.05
rcPML	no monotonic trend		greater than	1	1.90	0.17
rcPAP	no monotonic trend		greater than	1	0.27	0.6
rcMML	decreases from forest to plains	Forest, Plains, Mountain	greater than	1	78.09	<.05
rcMAP	no monotonic trend	Mountain	greater than	1	1.97	0.16
cMGML	increases from forest to plains	Plains	less than	1	34.51	<.05
rcPQML	decreases from forest to plains	Plains	greater than	1	79.98	<.05
cPQAP	no monotonic trend	Mountain	greater than	1	5.76	<.05
rcDQML	decreases from forest to plains	Forest, Mountain	greater than	1	53.42	<.05
cDQAP	decreases from forest to plains		greater than	1	32.49	<.05
rcEMAP	increases from forest to plains	Plains, Mountain	less than	1	31.67	<.05
rcMVAP	increases from forest to plains	Plains	less than	1	53.17	<.05
rcIMAP	increases from forest to plains	Mountain	less than	1	23.75	<.05
rcELAP	increases from forest to plains	Mountain	less than	1	18.89	<.05
rcLVAP	no monotonic trend		less than	1	39.31	<.05
rcILAP	increases from forest to plains	Forest, Mountain	less than	1	26.88	<.05
rcAVML	no monotonic trend	Plains, Mountain	less than	1	22.28	<.05
rcIVML	increases from forest to plains	Plains, Mountain	less than	1	25.36	<.05
rcPVML	no monotonic trend	Mountain	less than	1	6.85	<.05
rcADML	increases from forest to plains	Plains, Mountain	less than	1	20.71	<.05
rcIDML	no monotonic trend	Mountain	less than	1	5.22	<.05
rcPDML	no monotonic trend	Mountain	greater than	1	1.82	0.18
rcDDML	no monotonic trend	Mountain	greater than	1	12.78	<.05
rcDDAP	no monotonic trend		greater than	1	21.45	<.05
rcDEML	no monotonic trend	Mountain	greater than	1	9.66	<.05
cDEAP	no monotonic trend	Mountain	less than	1	0.02	0.88
rcIIML	no monotonic trend	Mountain	less than	1	2.02	0.16

Table 2.8: Morphology and habitat relationship by three criteria.

(C) Distal metatarsal variables.

Variable	Trend	Group Distinguished	Means Compared	*df*	χ^2	*P*
rINFANT	increases from forest to plains		less than	1	14.23	<.05
POSANT	no monotonic trend		greater than	1	0.27	0.6
rPOSINF	decreases from forest to plains		greater than	1	26.43	<.05
rdEMAP	no monotonic trend	Mountain	less than	1	0.44	0.51
rdMVAP	no monotonic trend		less than	1	37.83	<.05
rdIMAP	no monotonic trend	Mountain	less than	1	2.42	0.12
rdELAP	no monotonic trend	Mountain	less than	1	6.50	<.05
rdLVAP	no monotonic trend		less than	1	7.47	<.05
rdILAP	decreases from forest to plains	Plains, Mountain	greater than	1	19.99	<.05
rdAVML	no monotonic trend	Mountain	less than	1	3.70	0.05
rdIVML	no monotonic trend	Plains, Mountain	less than	1	28.14	<.05
rdPVML	no monotonic trend	Mountain	less than	1	3.44	0.06
rdADML	no monotonic trend	Plains, Mountain	less than	1	13.77	<.05
rdIDML	no monotonic trend	Plains, Mountain	less than	1	12.18	<.05
rdPDML	no monotonic trend	Mountain	greater than	1	0.01	0.93
rdDDML	no monotonic trend	Forest, Mountain	greater than	1	34.25	<.05
rdDDAP	no monotonic trend		greater than	1	42.06	<.05
rdDEML	no monotonic trend	Mountain	greater than	1	3.69	0.05
dDEAP	no monotonic trend		greater than	1	2.31	0.13
rdIIML	no monotonic trend	Plains, Mountain	less than	1	10.96	<.05

Table 2.8: Morphology and habitat relationship by three criteria.

(D) Distal metacarpal variables.

Variable	Trend	Group Distinguished	Means Compared	*df*	χ^2	*P*
rINFANT	increases from forest to plains		less than	1	1.04	0.31
POSANT	no monotonic trend		greater than	1	14.45	<.05
rPOSINF	decreases from forest to plains		greater than	1	24.47	<.05
rdEMAP	increases from forest to plains	Mountain	less than	1	7.89	<.05
rdMVAP	increases from forest to plains		less than	1	20.55	<.05
rdIMAP	no monotonic trend	Mountain	less than	1	0.87	0.35
rdELAP	no monotonic trend	Mountain	less than	1	2.37	0.12
rdLVAP	no monotonic trend		less than	1	10.91	<.05
rdILAP	no monotonic trend	Mountain	less than	1	1.79	0.18
rdAVML	no monotonic trend	Mountain	less than	1	4.84	<.05
rdIVML	no monotonic trend	Plains, Mountain	less than	1	9.39	<.05
rdPVML	no monotonic trend	Mountain	greater than	1	0.08	0.78
rdADML	no monotonic trend	Mountain	less than	1	4.30	<.05
rdIDML	no monotonic trend	Mountain	greater than	1	0.05	0.83
rdPDML	no monotonic trend	Forest, Mountain	greater than	1	13.34	<.05
rdDDML	decreases from forest to plains	Forest, Mountain	greater than	1	39.90	<.05
rdDDAP	no monotonic trend		greater than	1	42.69	<.05
rdDEML	decreases from forest to plains	Forest, Mountain	greater than	1	27.41	<.05
dDEAP	no monotonic trend	Mountain	greater than	1	4.64	<.05
rdIIML	no monotonic trend	Mountain	less than	1	0.28	0.59

Table 2.9: Canonical structure.

(A) Complete metatarsal.

Variable	CV1	CV2	CV1 (rotated 18.9°)	CV2 (rotated 24.3°)	CV3	CV4
rcMLEN	-0.68	-0.41	-0.52	-0.67	0.20	0.22
rcMML	0.81	0.17	0.72	0.51	0.16	-0.41
cPQML	0.79	-0.04	0.76	0.31	-0.11	-0.23
cPQAP	-0.37	-0.63	-0.17	-0.73	-0.21	-0.13
rcLVAP	-0.38	0.16	-0.41	-0.02	0.43	0.34
rcILAP	-0.18	-0.46	-0.04	-0.50	0.14	0.25
rcIDML	-0.09	0.74	-0.31	0.63	-0.25	-0.10
rcDDML	0.40	0.63	0.19	0.74	-0.31	0.20
rcDDAP	0.18	-0.54	0.33	-0.40	0.57	0.31
% Variance	51.9	39.4			7.6	1.1

(B) Complete metacarpal.

Variable	CV1	CV2	CV1 (rotated 52.1°)	CV2 (rotated 55.9°)	CV3	CV4
rcMLEN	-0.75	-0.01	-0.46	-0.61	0.46	0.15
rcMML	0.84	-0.11	0.61	0.60	-0.07	-0.37
rcEMAP	-0.80	-0.22	-0.33	-0.77	0.00	0.22
rcLVAP	-0.49	0.14	-0.42	-0.31	0.40	0.42
rcAVML	0.41	0.70	-0.29	0.74	-0.18	-0.12
rcADML	0.29	0.64	-0.32	0.62	-0.15	-0.04
rcDDML	0.75	0.35	0.20	0.81	-0.32	0.02
rcDDAP	0.01	-0.58	0.46	-0.34	0.30	0.59
rcDEML	0.55	0.18	0.21	0.55	-0.27	-0.11
% Variance	47.6	42.1			7.5	2.8

Table 2.9: Canonical structure.

(C) Distal metatarsal.

Variable	CV1	CV2	CV1 (rotated 39.2°)	CV2 (rotated 50.2°)	CV3
rdEMAP	0.53	0.63	0.06	0.80	0.07
rdMVAP	-0.22	0.47	-0.46	0.10	0.49
rdELAP	0.31	0.53	-0.06	0.56	0.30
rdILAP	0.61	0.32	0.31	0.68	0.09
rdADML	-0.55	-0.19	-0.33	-0.55	-0.28
rdIDML	-0.61	-0.33	-0.29	-0.68	-0.24
rdPDML	-0.48	-0.55	-0.06	-0.71	-0.14
rdDDAP	0.66	0.06	0.50	0.56	0.63
rdIIML	-0.51	-0.25	-0.27	-0.56	-0.41
% Variance	54.6	36.9			7.1

(D) Distal metacarpal.

Variable	CV1	CV2	CV1 (rotated 60.9°)	CV2 (rotated 64.0°)	CV3
rdEMAP	0.83	0.26	0.19	0.86	0.07
rdMVAP	0.39	-0.16	0.33	0.28	0.39
rdLVAP	0.38	-0.03	0.22	0.33	0.61
rdIVML	-0.46	-0.53	0.22	-0.64	-0.23
rdADML	-0.48	-0.46	0.16	-0.63	-0.19
rdDDML	-0.85	-0.04	-0.39	-0.79	-0.29
rdDDAP	-0.04	0.70	-0.63	0.26	0.46
rdDEML	-0.65	0.06	-0.37	-0.57	-0.26
rdIIML	-0.50	-0.39	0.09	-0.62	-0.50
% Variance	49.0	43.0			7.5

Table 2.10: Habitat classification with posterior probabilities for fossil bovid metapodials as variables are added to analyses.

(A) Complete metatarsal analysis.

Specimen	Number of Variables	Most likely habitat
YPM VP20693, Pikermi		
rcMML and rcIDML	2	Heavy cover [0.841]
rcLVAP added	3	Heavy cover [0.841]
rcMLEN added	4	Heavy cover [0.841]
rcDDML added	5	Heavy cover [0.841]
rcDDAP added	6	Heavy cover [0.841]
cPQML added	7	Heavy cover [0.841]
cPQAP added	8	Heavy cover [0.841]
rcILAP added	9	Heavy cover [0.841]
GSP 46737, Y0311		
rcMML and rcIDML	2	Heavy cover [0.73]
rcLVAP added	3	Heavy cover [0.73]
rcMLEN added	4	Heavy cover [0.73]
rcDDML added	5	Heavy cover [0.73]
rcDDAP added	6	Heavy cover [0.73]
cPQML added	7	Heavy cover [0.73]
cPQAP added	8	Heavy cover [0.73]
rcILAP added	9	Heavy cover [0.73]

Table 2.10: Habitat classification with posterior probabilities for fossil bovid metapodials as variables are added to analyses.

(B) Complete metacarpal analysis.

Specimen	Number of Variables	Most likely habitat
IPS BA 20617 , Ballestar		
rcMML and rcAVML	2	Heavy cover [0.564]
rcDDAP added	3	Heavy cover [0.564]
rcLVAP added	4	Heavy cover [0.564]
rcDDML added	5	Heavy cover [0.564]
rcEMAP added	6	Heavy cover [0.564]
rcADML added	7	Heavy cover [0.564]
rcMLEN added	8	Heavy cover [0.564]
rcDEML added	9	Heavy cover [0.564]
IPS CLL 20603, Can Llobateres		
rcMML and rcAVML	2	Light cover [0.717]
rcDDAP added	3	Light cover [0.717]
rcLVAP added	4	Light cover [0.717]
rcDDML added	5	Light cover [0.717]
rcEMAP added	6	Light cover [0.717]
rcADML added	7	Light cover [0.717]
rcMLEN added	8	Light cover [0.717]
rcDEML added	9	Light cover [0.717]
IPS 2548 , Can Llobateres		
rcMML and rcAVML	2	Heavy cover [0.816]
rcDDAP added	3	Heavy cover [0.816]
rcLVAP added	4	Heavy cover [0.816]
rcDDML added	5	Heavy cover [0.816]
rcEMAP added	6	Heavy cover [0.816]
rcADML added	7	Heavy cover [0.816]
rcMLEN added	8	Heavy cover [0.816]
rcDEML added	9	Heavy cover [0.816]
IPS 1237 , Torrent de Fibulines		
rcMML and rcAVML	2	Heavy cover [0.988]
rcDDAP added	3	Heavy cover [0.988]
rcLVAP added	4	Heavy cover [0.988]
rcDDML added	5	Heavy cover [0.988]
rcEMAP added	6	Heavy cover [0.988]
rcADML added	7	Heavy cover [0.988]
rcMLEN added	8	Heavy cover [0.988]
rcDEML added	9	Heavy cover [0.988]

GSP 46729, Y0311		
rcMML and rcAVML	2	Heavy cover [0.872]
rcDDAP added	3	Heavy cover [0.872]
rcLVAP added	4	Heavy cover [0.872]
rcDDML added	5	Heavy cover [0.872]
rcEMAP added	6	Heavy cover [0.872]
rcADML added	7	Heavy cover [0.872]
rcMLEN added	8	Heavy cover [0.872]
rcDEML added	9	Heavy cover [0.872]

Table 2.10: Habitat classification with posterior probabilities for fossil bovid metapodials as variables are added to analyses.

(C) Distal metatarsal analysis.

Specimen	Number of Variables	Most likely habitat
YPM VP20693, Pikermi		
rdEMAP and rdDDAP	2	Forest [0.329]
rdMVAP added	3	Forest [0.601]
rdIDML added	4	Forest [0.871]
rdILAP added	5	Forest [0.924]
rdELAP added	6	Forest [0.983]
rdADML added	7	Forest [0.98]
rdPDML added	8	Forest [0.982]
rdIIML added	9	Forest [0.999]
YPM VP20692, Pikermi		
rdEMAP and rdDDAP	2	Forest [0.371]
rdMVAP added	3	Forest [0.479]
rdIDML added	4	Heavy cover [0.507]
rdILAP added	5	Heavy cover [0.448]
rdELAP added	6	Heavy cover [0.412]
rdADML added	7	Heavy cover [0.548]
rdPDML added	8	Heavy cover [0.698]
rdIIML added	9	Heavy cover [0.638]
GSP32407 , Y0076		
rdEMAP and rdDDAP	2	Heavy cover [0.317]
rdMVAP added	3	Heavy cover [0.348]
rdIDML added	4	Mountain [0.341]
rdILAP added	5	Mountain [0.54]
rdELAP added	6	Mountain [0.69]
rdADML added	7	Mountain [0.62]
rdPDML added	8	Light cover [0.577]
rdIIML added	9	Forest [0.919]
GSP 46737, Y0311		
rdEMAP and rdDDAP	2	Heavy cover [0.324]
rdMVAP added	3	Heavy cover [0.369]
rdIDML added	4	Heavy cover [0.361]
rdILAP added	5	Heavy cover [0.427]
rdELAP added	6	Heavy cover [0.497]
rdADML added	7	Light cover [0.5]
rdPDML added	8	Light cover [0.538]
rdIIML added	9	Light cover [0.758]

GSP 47811, Y0311		
rdEMAP and rdDDAP	2	Heavy cover [0.342]
rdMVAP added	3	Light cover [0.434]
rdIDML added	4	Light cover [0.47]
rdILAP added	5	Light cover [0.609]
rdELAP added	6	Light cover [0.612]
rdADML added	7	Light cover [0.795]
rdPDML added	8	Light cover [0.805]
rdIIML added	9	Light cover [0.87]
GSP 47810, Y0311		
rdEMAP and rdDDAP	2	Forest [0.322]
rdMVAP added	3	Mountain [0.547]
rdIDML added	4	Mountain [0.597]
rdILAP added	5	Mountain [0.37]
rdELAP added	6	Mountain [0.336]
rdADML added	7	Light cover [0.34]
rdPDML added	8	Mountain [0.295]
rdIIML added	9	Mountain [0.309]
GSP26869 , Y0311		
rdEMAP and rdDDAP	2	Heavy cover [0.334]
rdMVAP added	3	Light cover [0.464]
rdIDML added	4	Light cover [0.45]
rdILAP added	5	Heavy cover [0.566]
rdELAP added	6	Heavy cover [0.472]
rdADML added	7	Light cover [0.494]
rdPDML added	8	Light cover [0.56]
rdIIML added	9	Light cover [0.822]
GSP45540 , Y0496		
rdEMAP and rdDDAP	2	Heavy cover [0.305]
rdMVAP added	3	Mountain [0.347]
rdIDML added	4	Mountain [0.428]
rdILAP added	5	Mountain [0.303]
rdELAP added	6	Heavy cover [0.301]
rdADML added	7	Light cover [0.514]
rdPDML added	8	Light cover [0.949]
rdIIML added	9	Light cover [0.892]
GSP45529 , Y0496		
rdEMAP and rdDDAP	2	Forest [0.338]
rdMVAP added	3	Plains [0.321]
rdIDML added	4	Heavy cover [0.485]
rdILAP added	5	Heavy cover [0.593]
rdELAP added	6	Heavy cover [0.654]
rdADML added	7	Heavy cover [0.702]
rdPDML added	8	Heavy cover [0.716]
rdIIML added	9	Heavy cover [0.983]

Table 2.10: Habitat classification with posterior probabilities for fossil bovid metapodials as variables are added to analyses.

(D) Distal metacarpal analysis.

Specimen	Number of Variables	Most likely habitat
IPS BA 20617 , Ballestar		
rdEMAP and rdDDAP	2	Heavy cover [0.432]
rdMVAP added	3	Mountain [0.424]
rdADML added	4	Heavy cover [0.508]
rdDDML added	5	Light cover [0.688]
rdDEML added	6	Light cover [0.581]
rdIVML added	7	Light cover [0.727]
rdIIML added	8	Light cover [0.99]
rdLVAP added	9	Light cover [0.967]
IPS CLL 20603, Can Llobateres		
rdEMAP and rdDDAP	2	Heavy cover [0.377]
rdMVAP added	3	Heavy cover [0.429]
rdADML added	4	Heavy cover [0.447]
rdDDML added	5	Light cover [0.386]
rdDEML added	6	Heavy cover [0.403]
rdIVML added	7	Forest [0.408]
rdIIML added	8	Heavy cover [0.602]
rdLVAP added	9	Heavy cover [0.739]
IPS 2548 , Can Llobateres		
rdEMAP and rdDDAP	2	Forest [0.307]
rdMVAP added	3	Forest [0.687]
rdADML added	4	Forest [0.503]
rdDDML added	5	Forest [0.776]
rdDEML added	6	Forest [0.959]
rdIVML added	7	Forest [0.822]
rdIIML added	8	Forest [0.817]
rdLVAP added	9	Forest [0.516]
IPS 1237 , Torrent de Fibulines		
rdEMAP and rdDDAP	2	Heavy cover [0.375]
rdMVAP added	3	Heavy cover [0.393]
rdADML added	4	Mountain [0.402]
rdDDML added	5	Heavy cover [0.557]
rdDEML added	6	Heavy cover [0.648]
rdIVML added	7	Heavy cover [0.498]
rdIIML added	8	Heavy cover [0.747]
rdLVAP added	9	Heavy cover [0.899]

GSP46146 , Y0076		
rdEMAP and rdDDAP	2	Heavy cover [0.423]
rdMVAP added	3	Heavy cover [0.533]
rdADML added	4	Heavy cover [0.513]
rdDDML added	5	Forest [0.523]
rdDEML added	6	Forest [0.572]
rdIVML added	7	Forest [0.499]
rdIIML added	8	Forest [1]
rdLVAP added	9	Forest [1]
GSP 46729, Y0311		
rdEMAP and rdDDAP	2	Heavy cover [0.373]
rdMVAP added	3	Heavy cover [0.492]
rdADML added	4	Heavy cover [0.491]
rdDDML added	5	Heavy cover [0.739]
rdDEML added	6	Heavy cover [0.733]
rdIVML added	7	Heavy cover [0.573]
rdIIML added	8	Heavy cover [0.549]
rdLVAP added	9	Heavy cover [0.828]
GSP 47806, Y0311		
rdEMAP and rdDDAP	2	Forest [0.363]
rdMVAP added	3	Heavy cover [0.467]
rdADML added	4	Heavy cover [0.527]
rdDDML added	5	Heavy cover [0.617]
rdDEML added	6	Heavy cover [0.623]
rdIVML added	7	Heavy cover [0.541]
rdIIML added	8	Light cover [0.616]
rdLVAP added	9	Heavy cover [0.58]
GSP 47808, Y0311		
rdEMAP and rdDDAP	2	Heavy cover [0.379]
rdMVAP added	3	Mountain [0.48]
rdADML added	4	Mountain [0.6]
rdDDML added	5	Mountain [0.677]
rdDEML added	6	Forest [0.462]
rdIVML added	7	Light cover [0.373]
rdIIML added	8	Forest [0.543]
rdLVAP added	9	Forest [0.67]
GSP 47807, Y0311		
rdEMAP and rdDDAP	2	Heavy cover [0.328]
rdMVAP added	3	Heavy cover [0.363]
rdADML added	4	Heavy cover [0.445]
rdDDML added	5	Heavy cover [0.564]
rdDEML added	6	Heavy cover [0.62]
rdIVML added	7	Heavy cover [0.611]
rdIIML added	8	Heavy cover [0.582]
rdLVAP added	9	Heavy cover [0.644]

GSP 47809, Y0311		
rdEMAP and rdDDAP	2	Forest [0.346]
rdMVAP added	3	Heavy cover [0.438]
rdADML added	4	Heavy cover [0.416]
rdDDML added	5	Heavy cover [0.622]
rdDEML added	6	Heavy cover [0.645]
rdIVML added	7	Heavy cover [0.785]
rdIIML added	8	Heavy cover [0.536]
rdLVAP added	9	Heavy cover [0.87]
GSP12203 , Y0311		
rdEMAP and rdDDAP	2	Forest [0.426]
rdMVAP added	3	Heavy cover [0.552]
rdADML added	4	Forest [0.726]
rdDDML added	5	Forest [0.82]
rdDEML added	6	Forest [0.8]
rdIVML added	7	Forest [0.644]
rdIIML added	8	Forest [0.808]
rdLVAP added	9	Forest [0.793]
GSP14101 , Y0311		
rdEMAP and rdDDAP	2	Forest [0.353]
rdMVAP added	3	Heavy cover [0.397]
rdADML added	4	Heavy cover [0.421]
rdDDML added	5	Heavy cover [0.621]
rdDEML added	6	Heavy cover [0.653]
rdIVML added	7	Light cover [0.717]
rdIIML added	8	Light cover [0.694]
rdLVAP added	9	Light cover [0.791]
GSP6477, Y0311		
rdEMAP and rdDDAP	2	Forest [0.422]
rdMVAP added	3	Heavy cover [0.548]
rdADML added	4	Heavy cover [0.656]
rdDDML added	5	Light cover [0.618]
rdDEML added	6	Light cover [0.575]
rdIVML added	7	Light cover [0.856]
rdIIML added	8	Light cover [0.959]
rdLVAP added	9	Light cover [0.759]
GSP12154 , Y0311		
rdEMAP and rdDDAP	2	Forest [0.314]
rdMVAP added	3	Light cover [0.554]
rdADML added	4	Light cover [0.575]
rdDDML added	5	Light cover [0.666]
rdDEML added	6	Light cover [0.743]
rdIVML added	7	Light cover [0.944]
rdIIML added	8	Light cover [0.948]
rdLVAP added	9	Light cover [0.958]

GSP10569 , Y0311		
rdEMAP and rdDDAP	2	Heavy cover [0.414]
rdMVAP added	3	Heavy cover [0.513]
rdADML added	4	Heavy cover [0.591]
rdDDML added	5	Heavy cover [0.572]
rdDEML added	6	Heavy cover [0.629]
rdIVML added	7	Heavy cover [0.709]
rdIIML added	8	Forest [0.898]
rdLVAP added	9	Forest [0.492]
GSP45524 , Y0496		
rdEMAP and rdDDAP	2	Mountain [0.332]
rdMVAP added	3	Mountain [0.803]
rdADML added	4	Mountain [0.885]
rdDDML added	5	Mountain [0.953]
rdDEML added	6	Mountain [0.873]
rdIVML added	7	Mountain [0.614]
rdIIML added	8	Mountain [0.505]
rdLVAP added	9	Mountain [0.909]
GSP45541 , Y0496		
rdEMAP and rdDDAP	2	Heavy cover [0.409]
rdMVAP added	3	Heavy cover [0.457]
rdADML added	4	Heavy cover [0.508]
rdDDML added	5	Heavy cover [0.758]
rdDEML added	6	Heavy cover [0.561]
rdIVML added	7	Light cover [0.816]
rdIIML added	8	Light cover [0.819]
rdLVAP added	9	Light cover [0.867]

Table 2.11: Species with one half or more of individuals reclassified in one analysis.

Species	Number reclassified/total number*	Original habitat	Most likely reclassification†
Alcelaphus lichtensteini	1 / 1 [CMT]	Plains	Light cover (1)
Tragelaphus derbianus	1 / 1 [CMT]	Light cover	Heavy cover (1)
Kobus leche	1 / 1 [CMC]	Light cover	Heavy cover (1)
Ovis ammon	4 / 5 [CMC]	Mountain	Light cover (1), Plains (3)
Gazella gazella	1 / 1 [DMT]	Plains	Heavy cover (1)
Madoqua sp.	2 / 3 [DMT]	Heavy cover	Light cover (1), Plains (1)
Bos gaurus	3 / 5 [DMT]	Heavy cover	Forest (3)
Hippotragus niger	6 / 6 [DMT]	Light cover	Forest (1), Heavy cover (1), Plains (3)
Cephalophus weynsi	1 / 1 [DMC]	Forest	Light cover (1)
Oryx dammah	2 / 2 [DMC]	Plains	Heavy cover (1), Light cover (1)
Raphicerus campestris	3 / 5 [DMC]	Light cover	Heavy cover (2), Plains (1)
Ourebia ourebi	4 / 7 [DMC]	Light cover	Heavy cover (1), Plains (3)

*[CMT] is the complete metatarsal analysis, [CMC] is complete metacarpal analysis, [DMT] is the distal metatarsal analysis, [DMC] is the distal metacarpal analysis.
†( ) is the number of individuals reclassified to that habitat.

Table 2.12: Species with one half or more of individuals reclassified in more than one analysis.

Species	Number reclassified/total number*	Original habitat	Most likely reclassification†
Bison bison athabaskae	4 / 5 [CMT]	Light cover	Heavy cover (2), Mountain (2)
	5 / 5 [DMC]	Light cover	Plains (1), Mountain (4)
	5 / 5 [DMT]	Light cover	Heavy cover (2), Plains (3)
Bison bison bison	4 / 5 [CMC]	Plains	Forest (2), Light cover (1), Mountain (1)
	4 / 6 [CMT]	Plains	Heavy cover (3), Light cover (1)
Bubalis bubalis	1 / 1 [CMC]	Heavy cover	Forest (1)
	1 / 1 [DMC]	Heavy cover	Forest (1)
Kobus ellipsiprymnus	5 / 8 [CMC]	Heavy cover	Light cover (3), Plains (2)
	4 / 7 [DMT]	Heavy cover	Light cover (4)
Kobus megaceros	4 / 6 [CMC]	Heavy cover	Light cover (3), Plains (1)
	5 / 6 [CMT]	Heavy cover	Light cover (5)
Kobus megaceros	4 / 6 [DMT]	Heavy cover	Light cover (3), Plains (1)
Madoqua guentheri	3 / 3 [CMT]	Heavy cover	Light cover (2), Plains (1)
	2 / 3 [DMC]	Heavy cover	Light cover (1), Plains (1)
	2 / 3 [DMT]	Heavy cover	Plains (2)

Madoqua kirki	5 / 6 [CMC]	Heavy cover	Light cover (3), Plains (2)
	4 / 6 [DMC]	Heavy cover	Forest (1), Plains (3)
	5 / 6 [DMT]	Heavy cover	Light cover (1), Plains (4)
Neotragus batesi	1 / 1 [CMT]	Forest	Mountain (1)
	1 / 1 [DMT]	Forest	Mountain (1)
Raphicerus sharpei	1 / 1 [CMT]	Light cover	Heavy cover (1)
	1 / 1 [DMC]	Light cover	Heavy cover (1)
Sylvicapra grimmia	7 / 9 [CMC]	Light cover	Forest (7)
	5 / 9 [DMC]	Light cover	Forest (4), Heavy cover (1)
Syncerus caffer caffer	3 / 3 [CMC]	Light cover	Forest (2), Mountain (1)
	3 / 3 [CMT]	Light cover	Forest (2), Mountain (1)
	3 / 3 [DMC]	Light cover	Forest (2), Heavy cover (1)
	3 / 3 [DMT]	Light cover	Forest (1), Heavy cover (1), Mountain (1)
Syncerus caffer nanus	2 / 3 [CMC]	Heavy cover	Forest (2)
	3 / 3 [CMT]	Heavy cover	Light cover (1), Mountain (2)
	2 / 3 [DMC]	Heavy cover	Forest (1), Plains (1)

*[CMT] is the complete metatarsal analysis, [CMC] is complete metacarpal analysis, [DMT] is the distal metatarsal analysis, [DMC] is the distal metacarpal analysis.

†() is the number of individuals reclassified to that habitat.

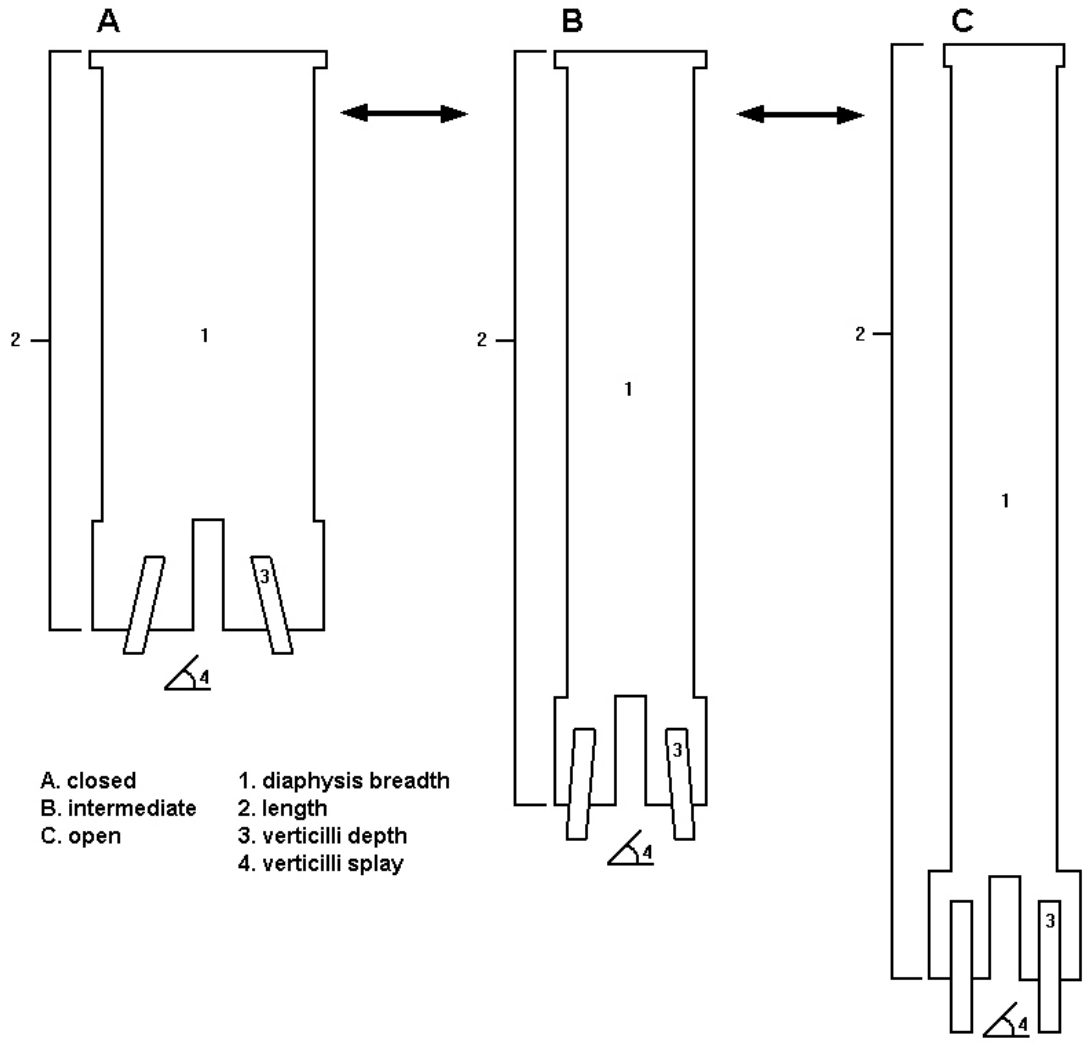


Figure 2.1: Schematic of bovid metapodial morphology.

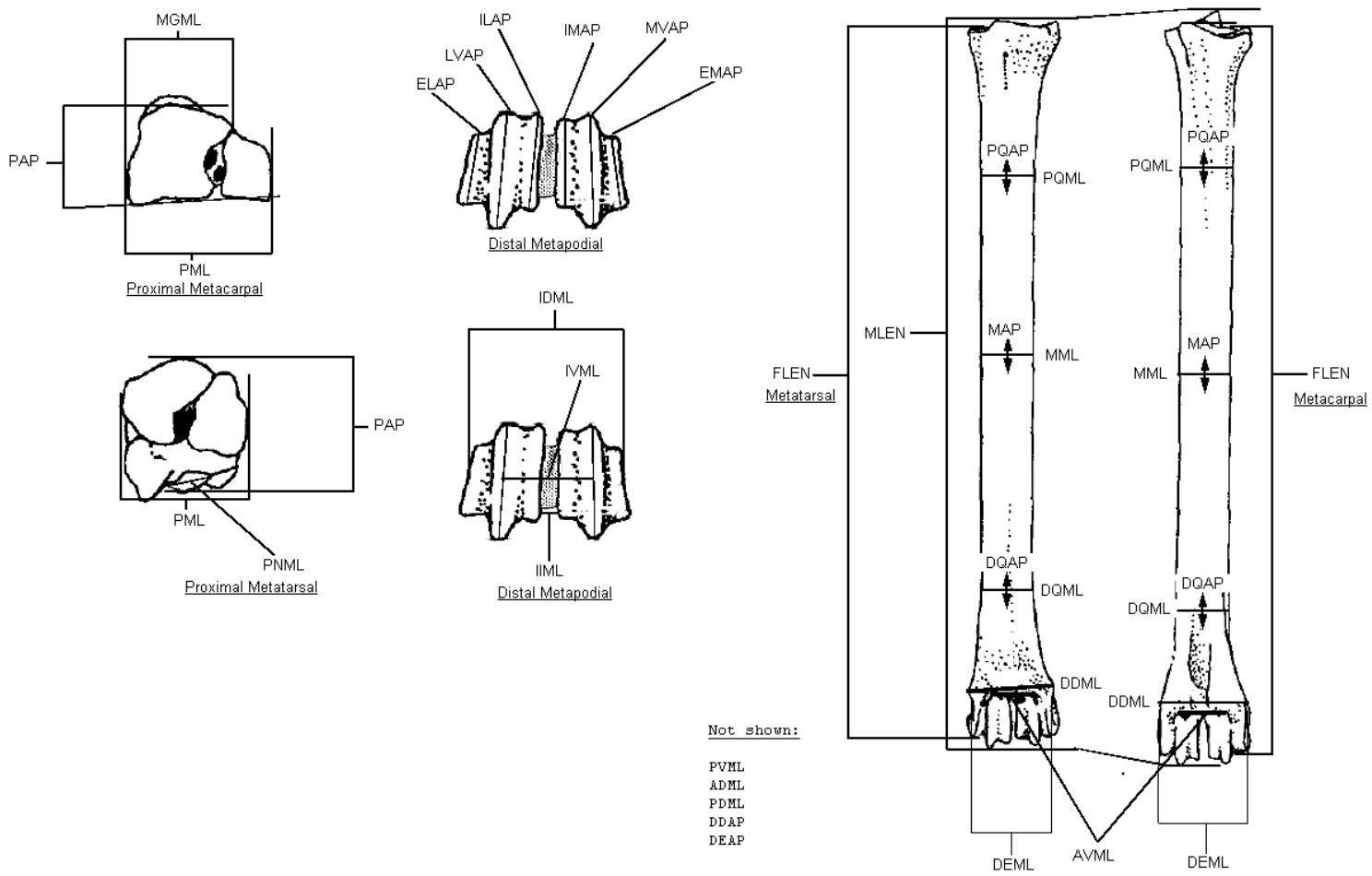


Figure 2.2: Measurements taken on bovid metapodials. Diagram after Plummer and Bishop (1994).

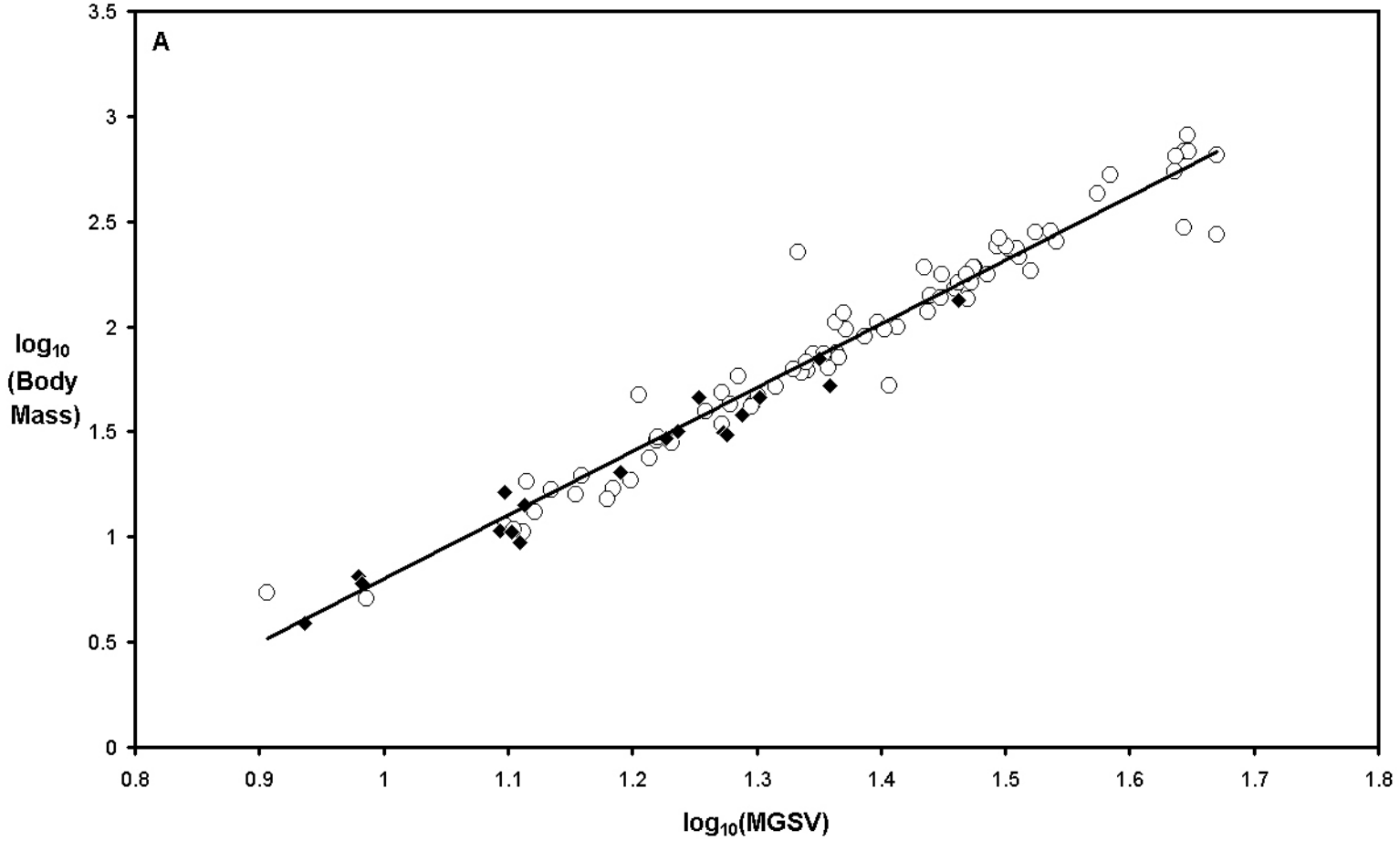


Figure 2.3: Bovid body mass versus metapodial size. A, complete metatarsals; B, complete metacarpals; C, distal metatarsals; D, distal metacarpals. Species means reported for bovid body mass are regressed against species means of MGSV and DMGSV. Species mean data points are shown as open circles (○). Data points for body masses and MGSV or DMGSV for individual specimens of the Yale Peabody Museum bovids collected by Roland Bauer are also plotted and shown as filled diamonds (◆).

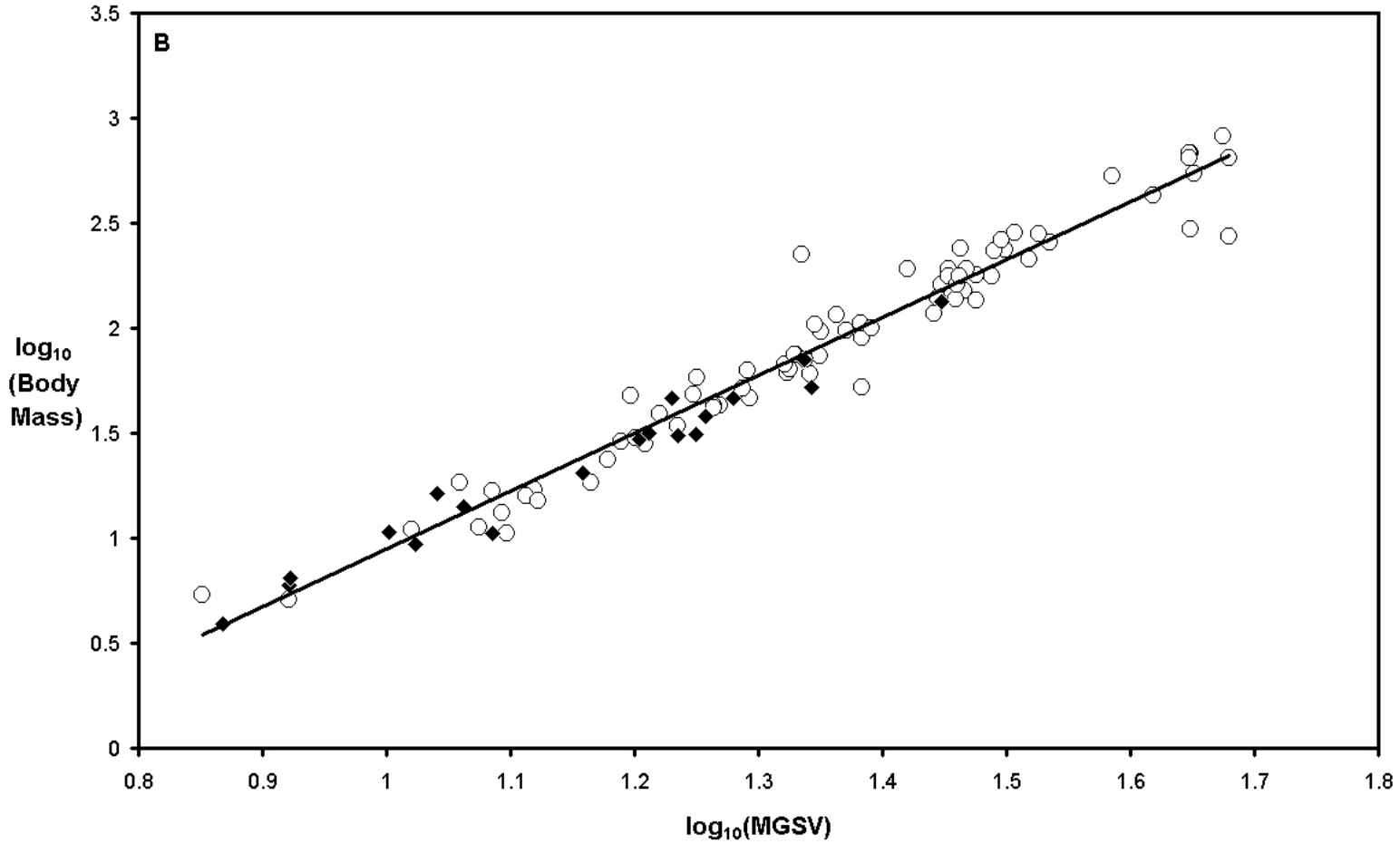


Figure 2.3: Bovid body mass versus metapodial size. A, complete metatarsals; B, complete metacarpals; C, distal metatarsals; D, distal metacarpals. Species means reported for bovid body mass are regressed against species means of MGSV and DMGSV. Species mean data points are shown as open circles (○). Data points for body masses and MGSV or DMGSV for individual specimens of the Yale Peabody Museum bovids collected by Roland Bauer are also plotted and shown as filled diamonds (◆).

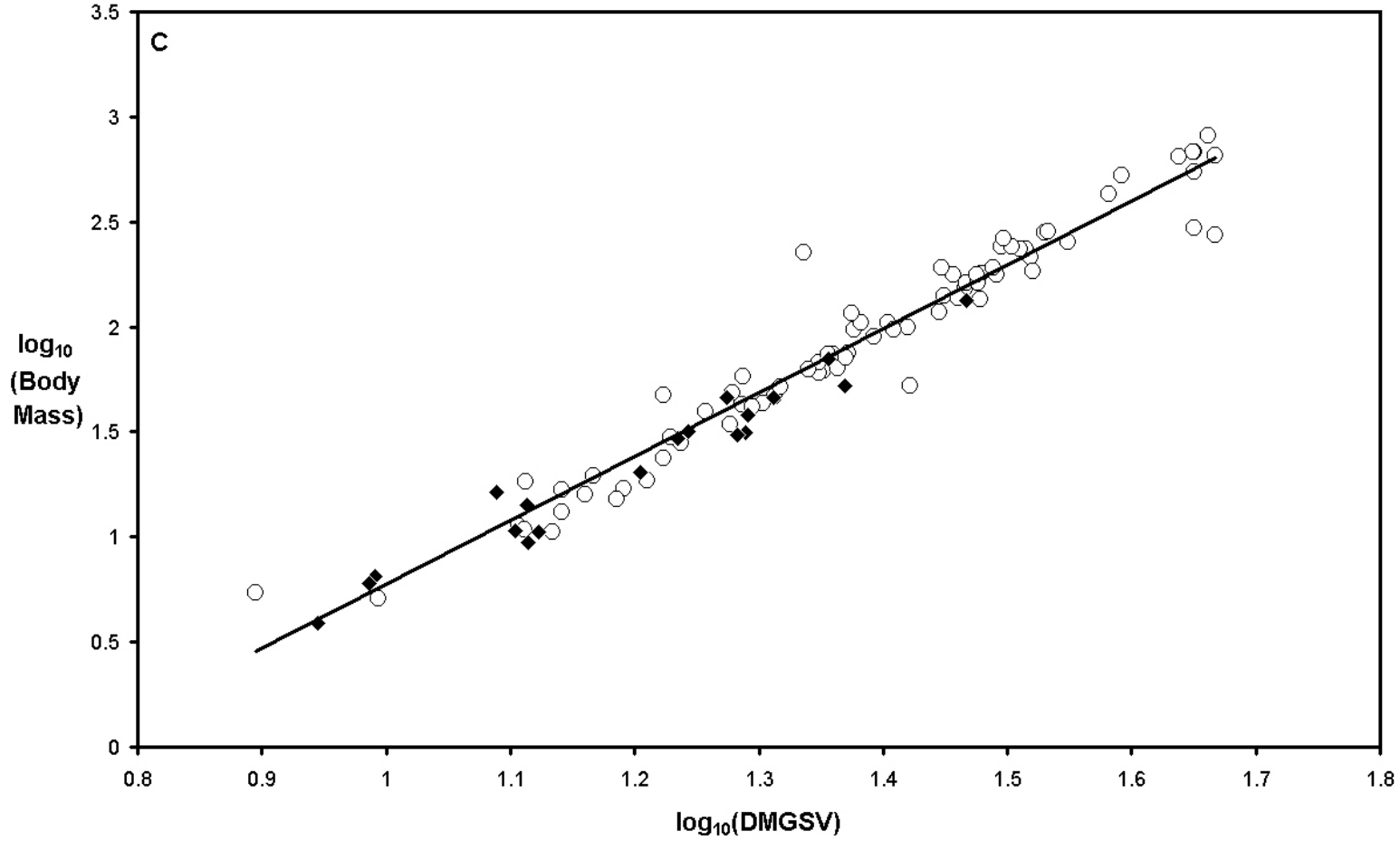


Figure 2.3: Bovid body mass versus metapodial size. A, complete metatarsals; B, complete metacarpals; C, distal metatarsals; D, distal metacarpals. Species means reported for bovid body mass are regressed against species means of MGSV and DMGSV. Species mean data points are shown as open circles (○). Data points for body masses and MGSV or DMGSV for individual specimens of the Yale Peabody Museum bovids collected by Roland Bauer are also plotted and shown as filled diamonds (◆).

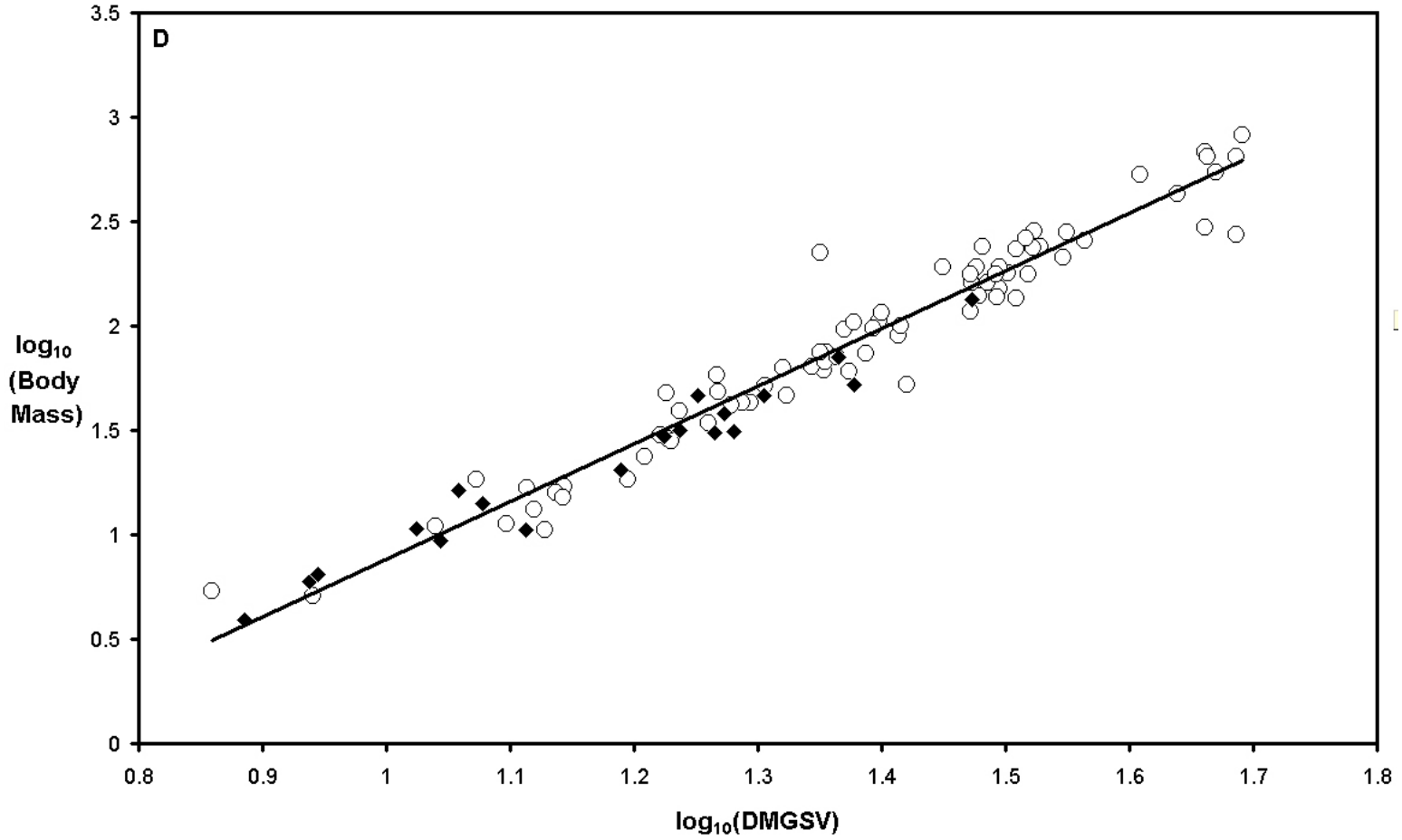


Figure 2.3: Bovid body mass versus metapodial size. A, complete metatarsals; B, complete metacarpals; C, distal metatarsals; D, distal metacarpals. Species means reported for bovid body mass are regressed against species means of MGSV and DMGSV. Species mean data points are shown as open circles (○). Data points for body masses and MGSV or DMGSV for individual specimens of the Yale Peabody Museum bovids collected by Roland Bauer are also plotted and shown as filled diamonds (◆).

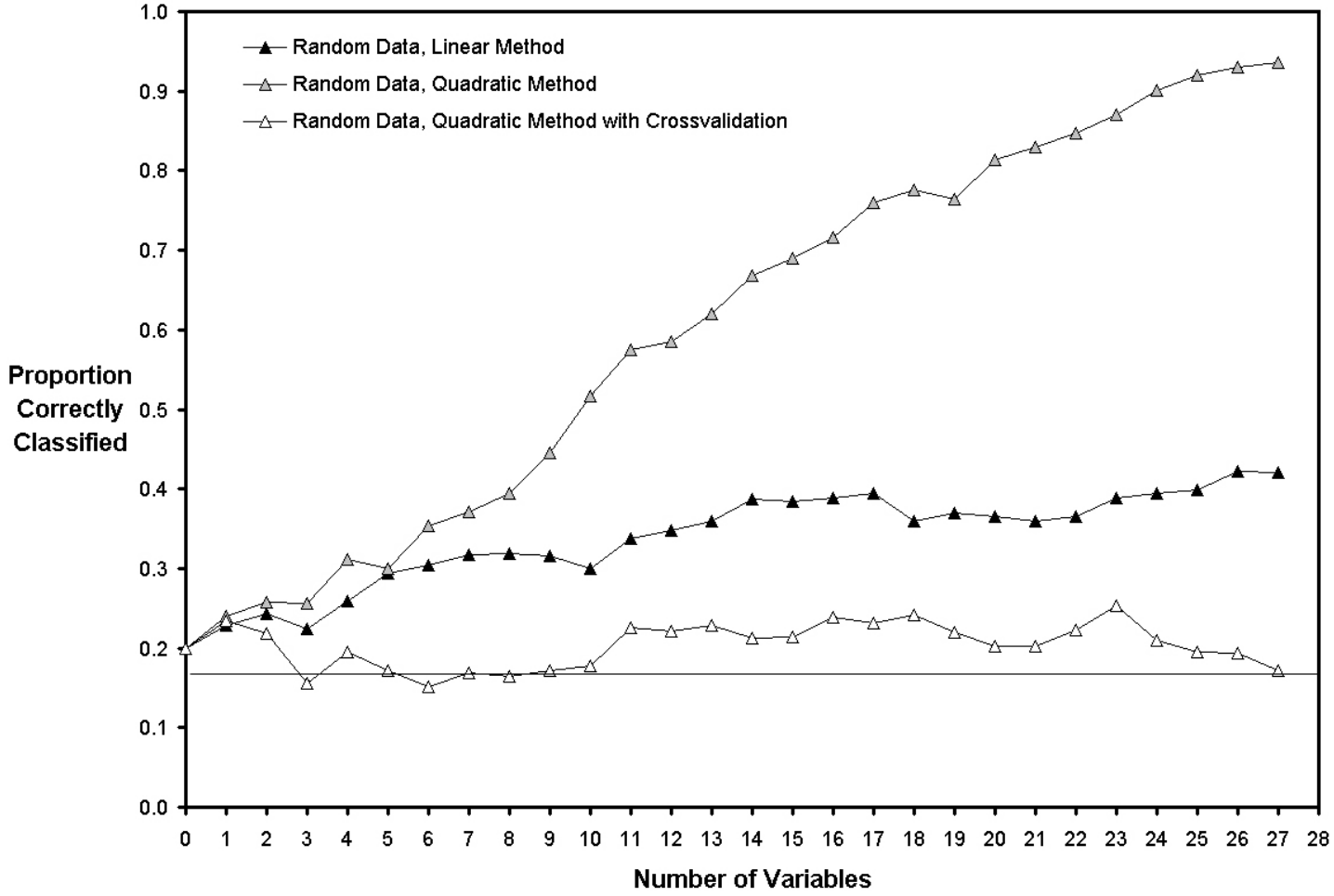


Figure 2.4: Random simulation showing the effects of variable number on correct classification. The proportion of correctly classified cases versus number of predictor variables for linear and quadratic discriminant function analyses of a randomly generated data set of normally distributed variables assigned to five groups with sample sizes comparable to those of the complete metatarsal data set. The quadratic analysis is shown with and without crossvalidation.

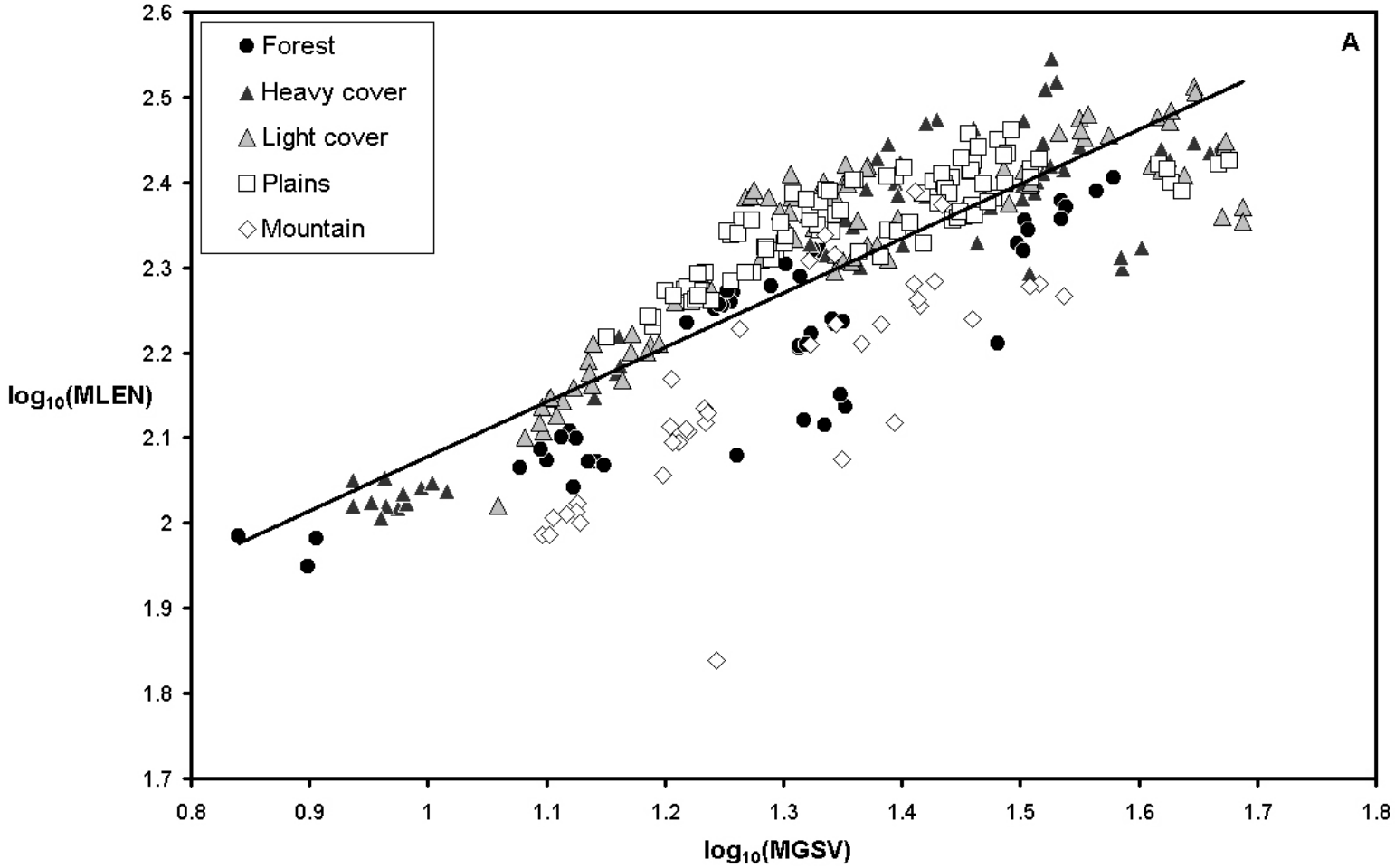


Figure 2.5: Least squares regression of $\log_{10}$(MLEN) versus $\log_{10}$(MGSV). A, metatarsals; B, metacarpals. The complete bovid-antilocaprid samples are shown by habitat group with the best fit least squares regression line for $\log_{10}$(MLEN) versus $\log_{10}$(MGSV).

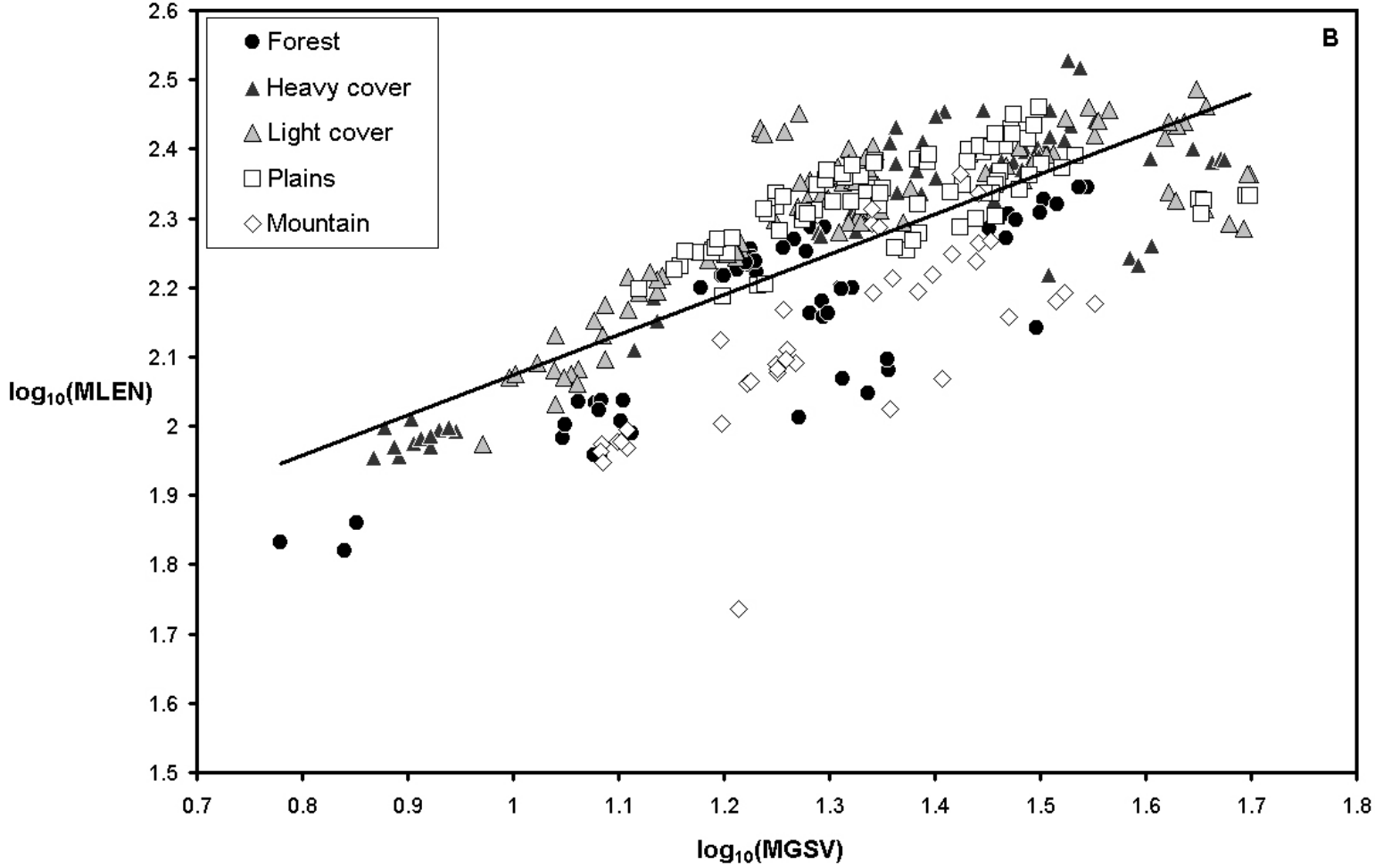


Figure 2.5: Least squares regression of $\log_{10}$(MLEN) versus $\log_{10}$(MGSV). A, metatarsals; B, metacarpals. The complete bovid-antilocaprid samples are shown by habitat group with the best fit least squares regression line for $\log_{10}$(MLEN) versus $\log_{10}$(MGSV).

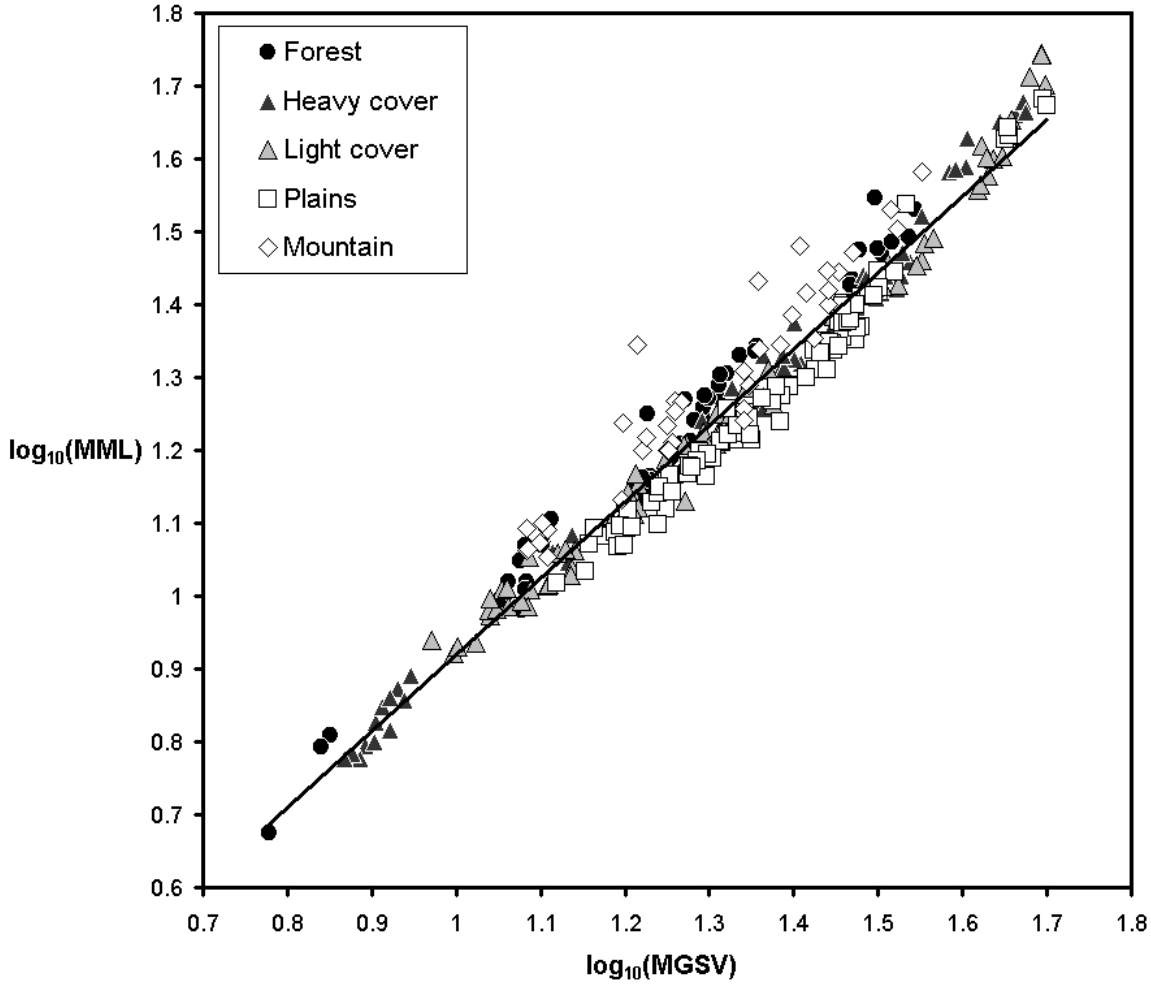


Figure 2.6: Least squares regression of log10(MML) versus log10(MGSV) for metacarpals.

The complete bovid-antilocaprid metacarpal sample is shown by habitat group with the best fit least squares regression line for $\log_{10}$(MML) versus $\log_{10}$(MGSV).

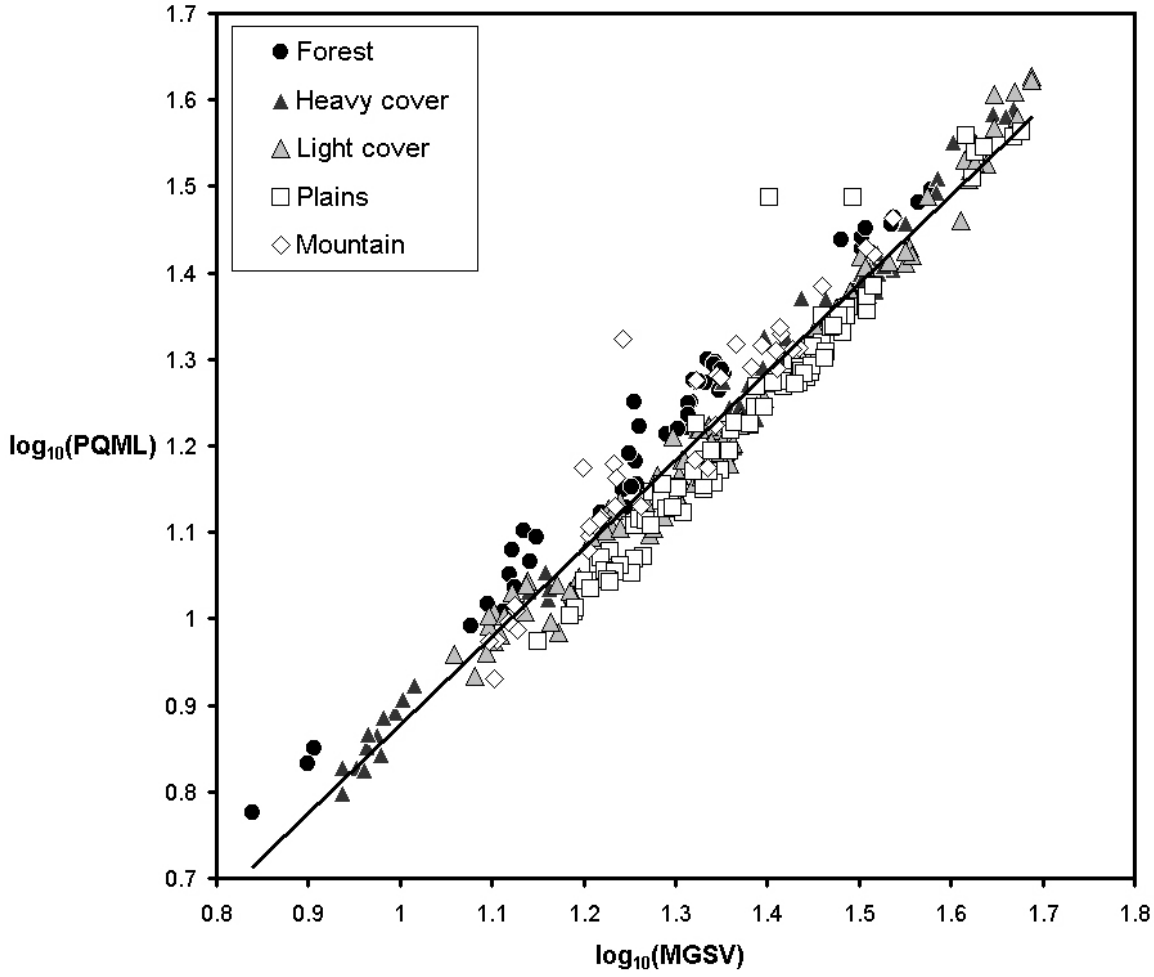


Figure 2.7: Least squares regression of log10(PQML) versus log10(MGSV) for metatarsals.

The complete bovid-antilocaprid metatarsal sample is shown by habitat group with the best fit least squares regression line for $\log_{10}$(PQML) versus $\log_{10}$(MGSV).

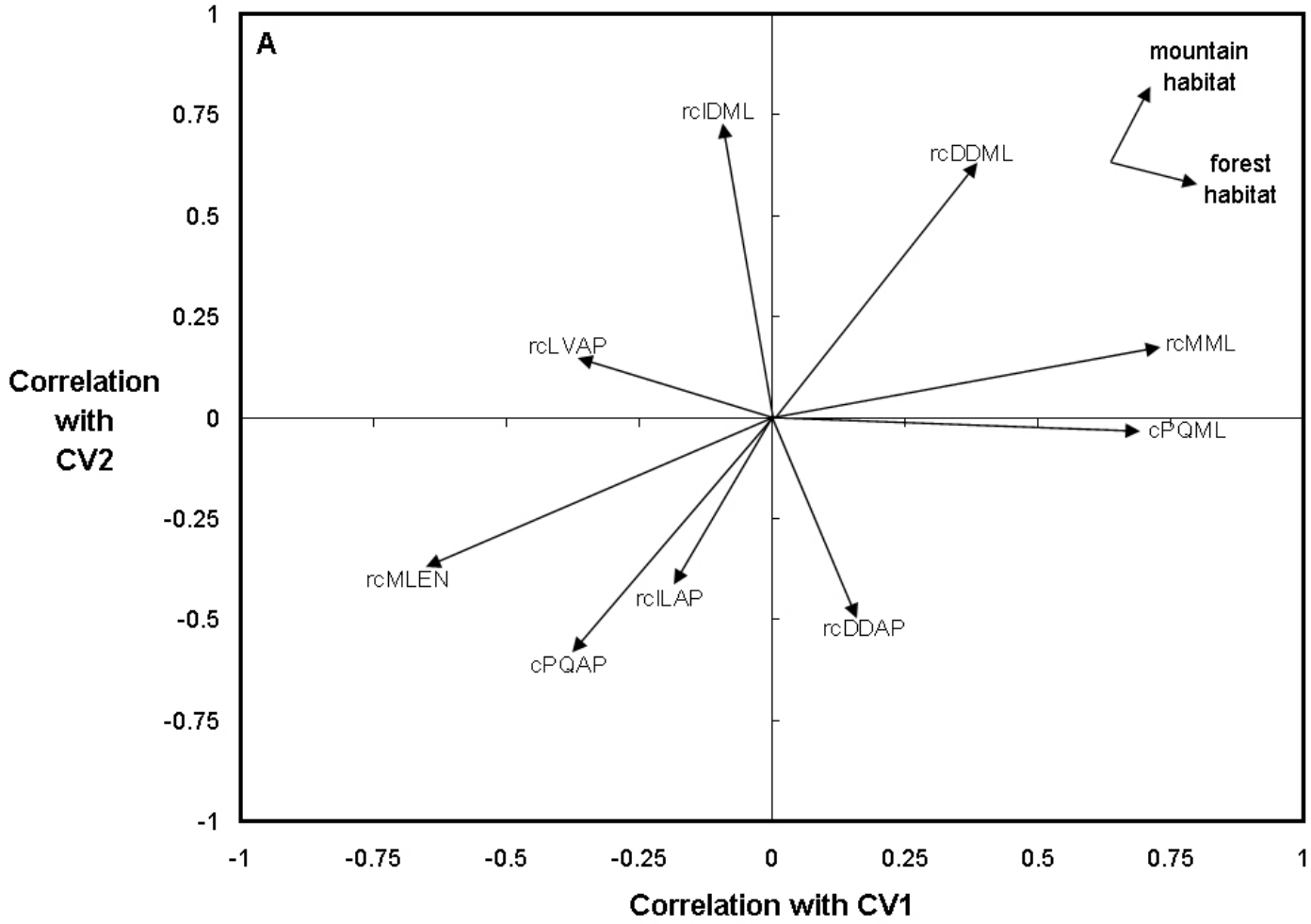


Figure 2.8: Total canonical structure for canonical variables one and two. A, complete metatarsal analysis; B, complete metacarpal analysis. The correlations for each morphological variable with the first two canonical variables are plotted and a vector drawn representing the relationship between each morphological variable and the two-dimensional canonical variable space capturing the majority of habitat related variability.

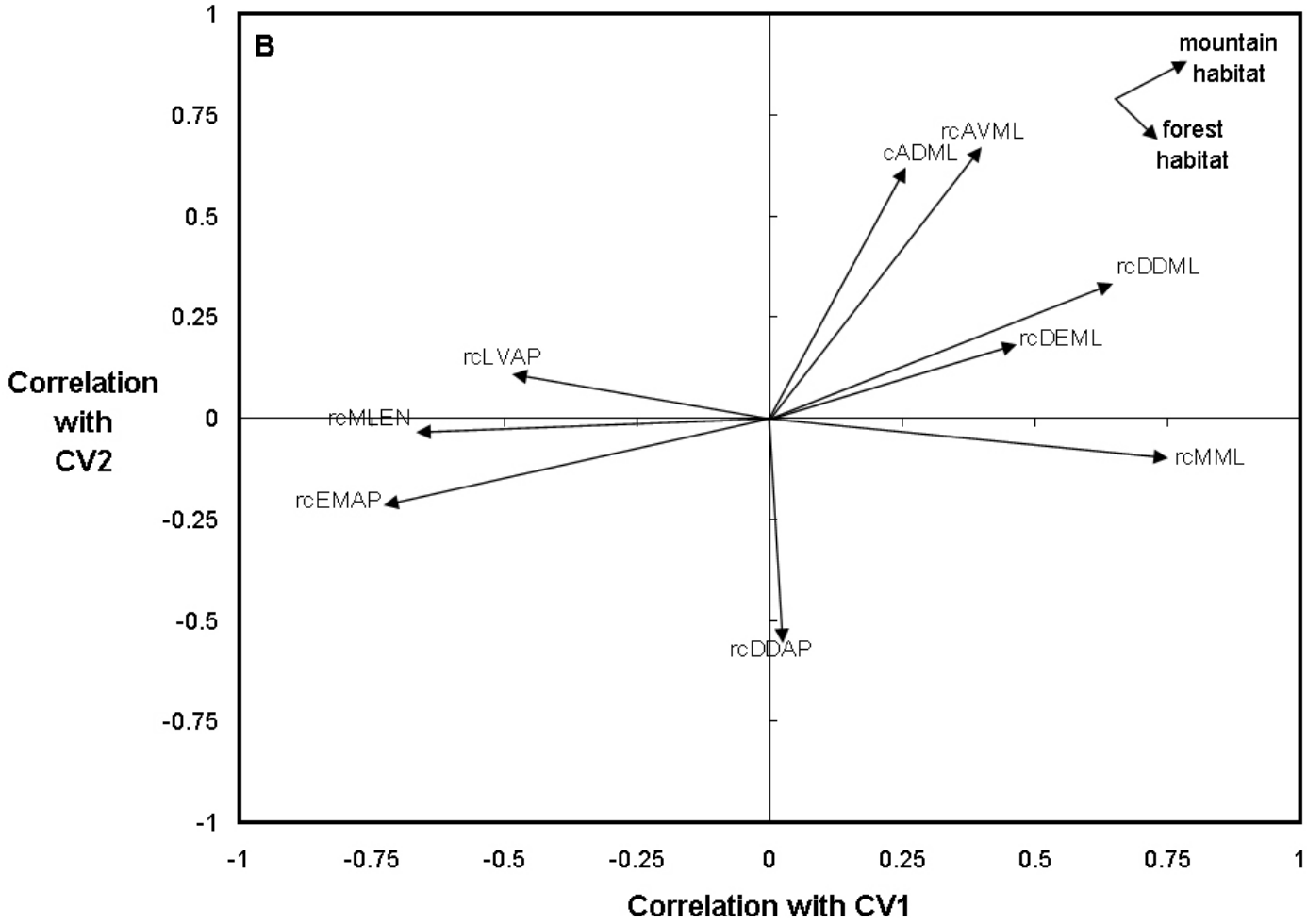


Figure 2.8: Total canonical structure for canonical variables one and two. A, complete metatarsal analysis; B, complete metacarpal analysis. The correlations for each morphological variable with the first two canonical variables are plotted and a vector drawn representing the relationship between each morphological variable and the two-dimensional canonical variable space capturing the majority of habitat related variability.

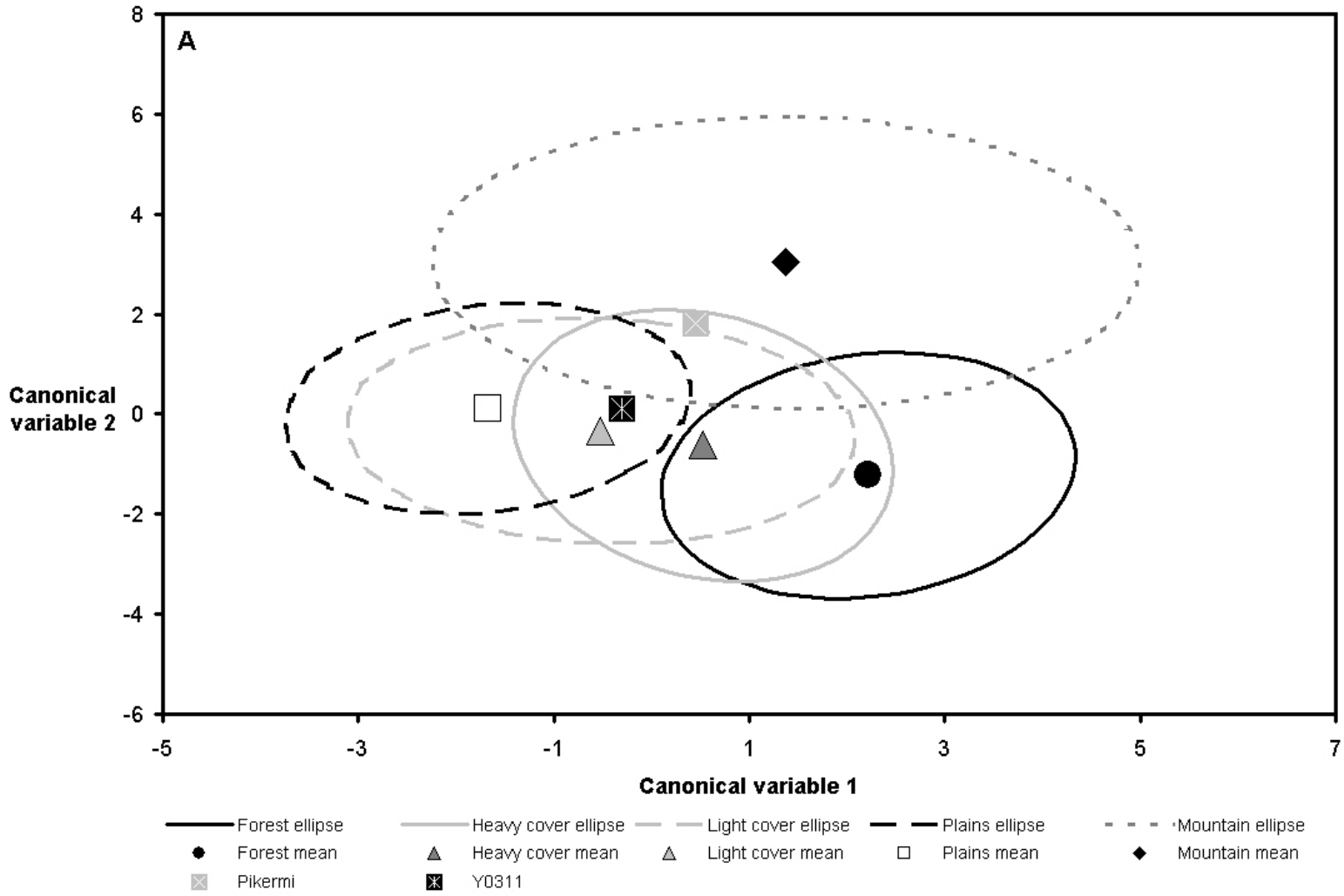


Figure 2.9: Bivariate plot of CV1 and CV2. A, complete metatarsals; B, complete metacarpals; C, distal metatarsals; D, distal metacarpals. Habitat group means, fossil specimens, and 95% confidence ellipses of each habitat group are plotted for CV1 and CV2.

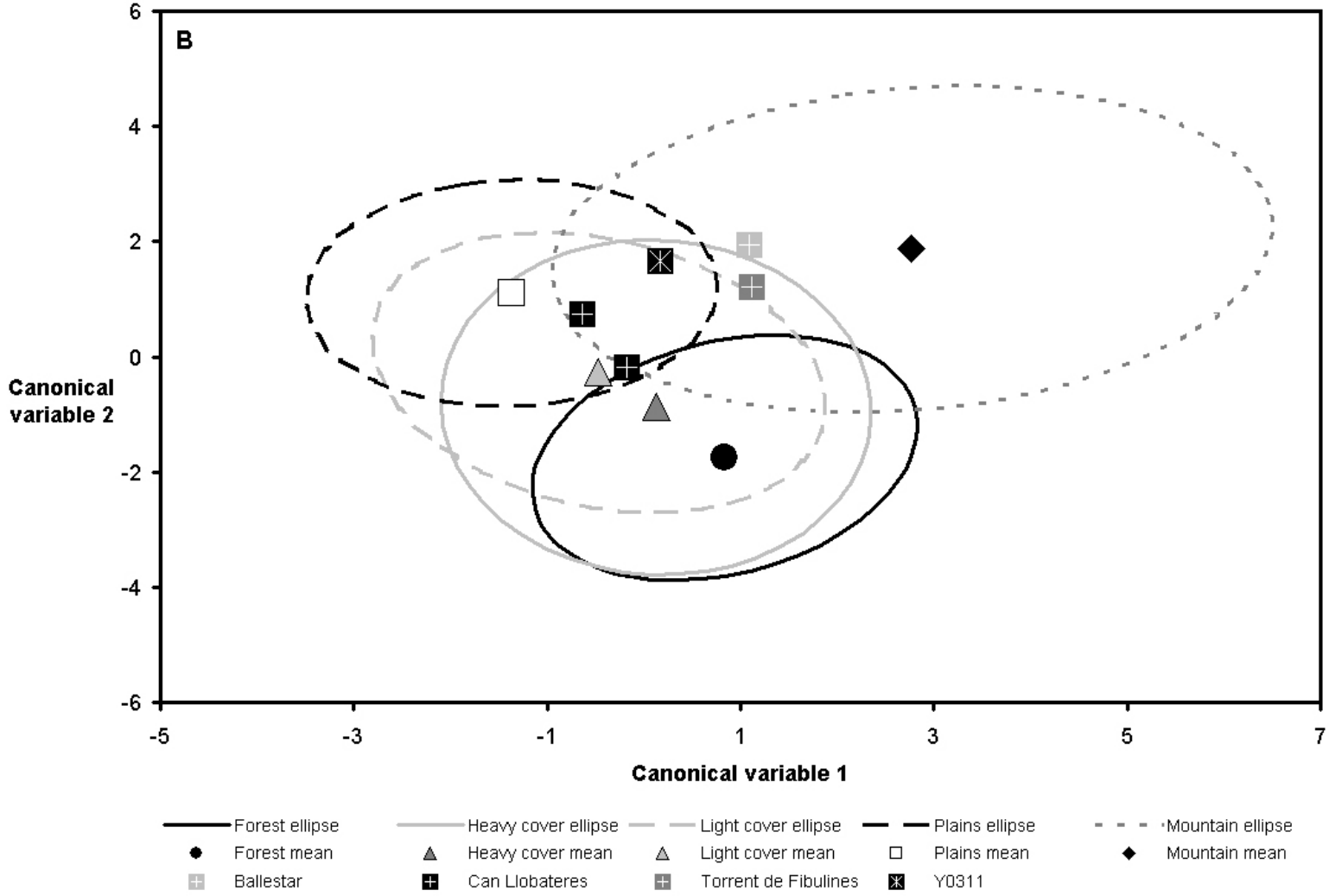


Figure 2.9: Bivariate plot of CV1 and CV2. A, complete metatarsals; B, complete metacarpals; C, distal metatarsals; D, distal metacarpals. Habitat group means, fossil specimens, and 95% confidence ellipses of each habitat group are plotted for CV1 and CV2.

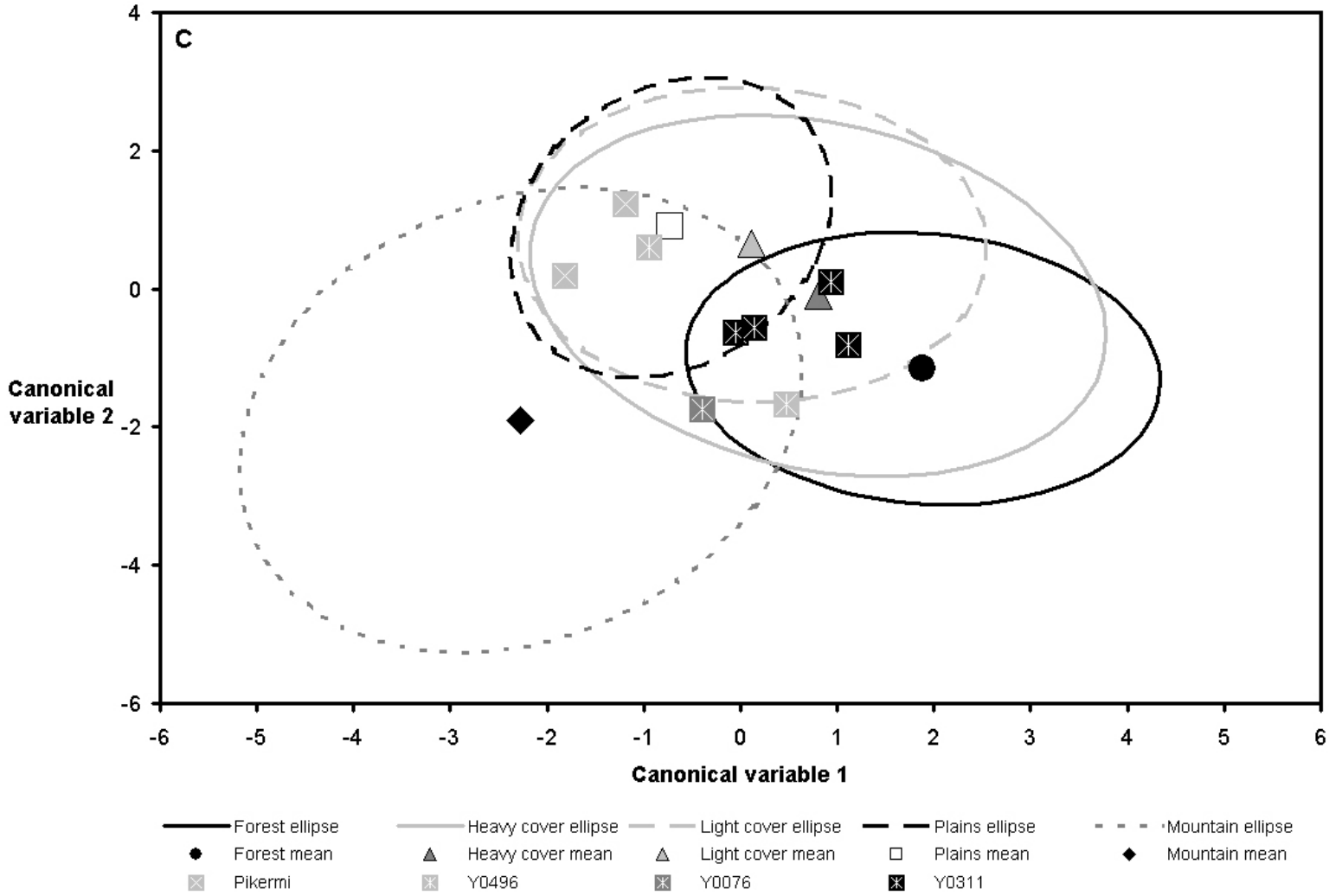


Figure 2.9: Bivariate plot of CV1 and CV2. A, complete metatarsals; B, complete metacarpals; C, distal metatarsals; D, distal metacarpals. Habitat group means, fossil specimens, and 95% confidence ellipses of each habitat group are plotted for CV1 and CV2.

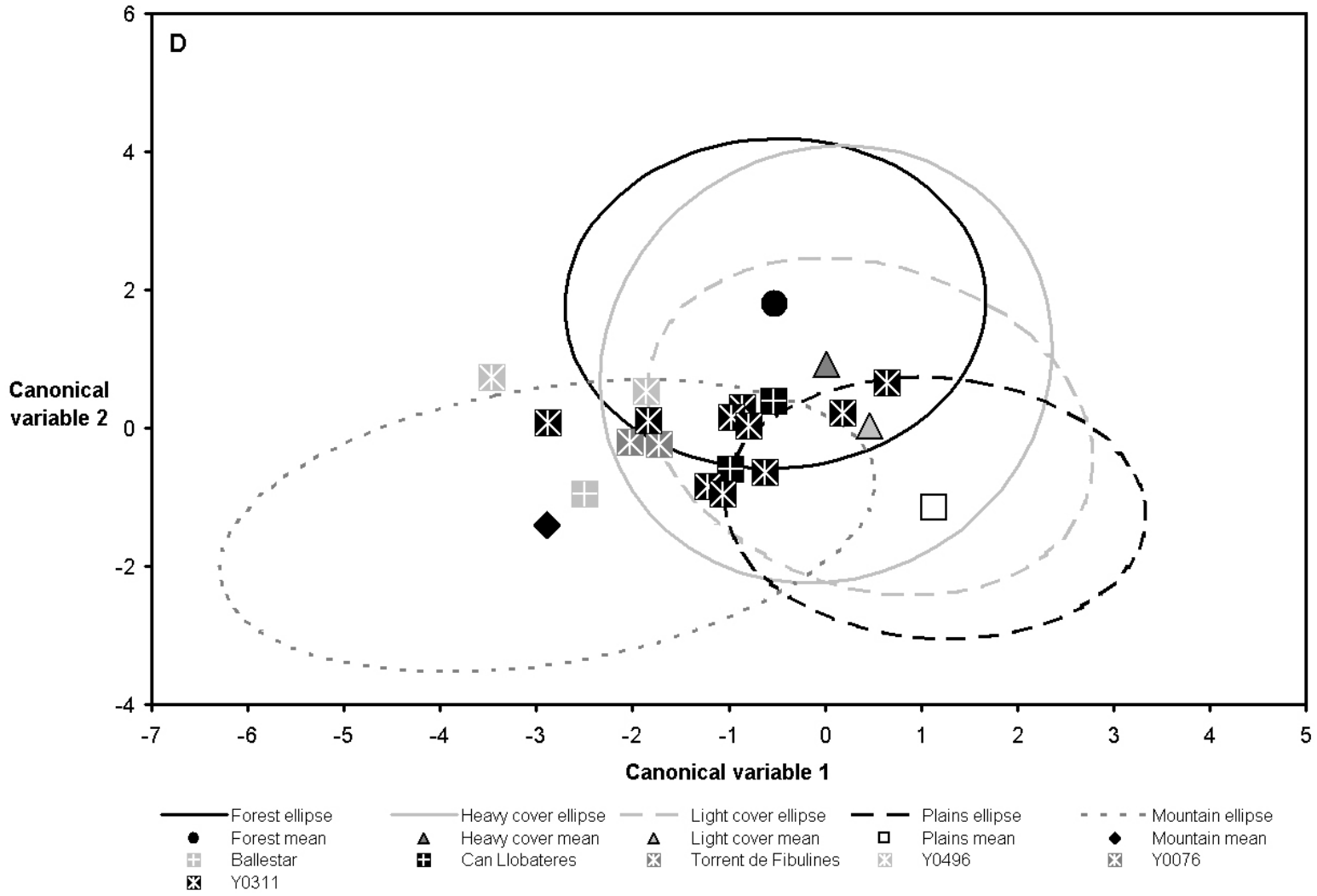


Figure 2.9: Bivariate plot of CV1 and CV2. A, complete metatarsals; B, complete metacarpals; C, distal metatarsals; D, distal metacarpals. Habitat group means, fossil specimens, and 95% confidence ellipses of each habitat group are plotted

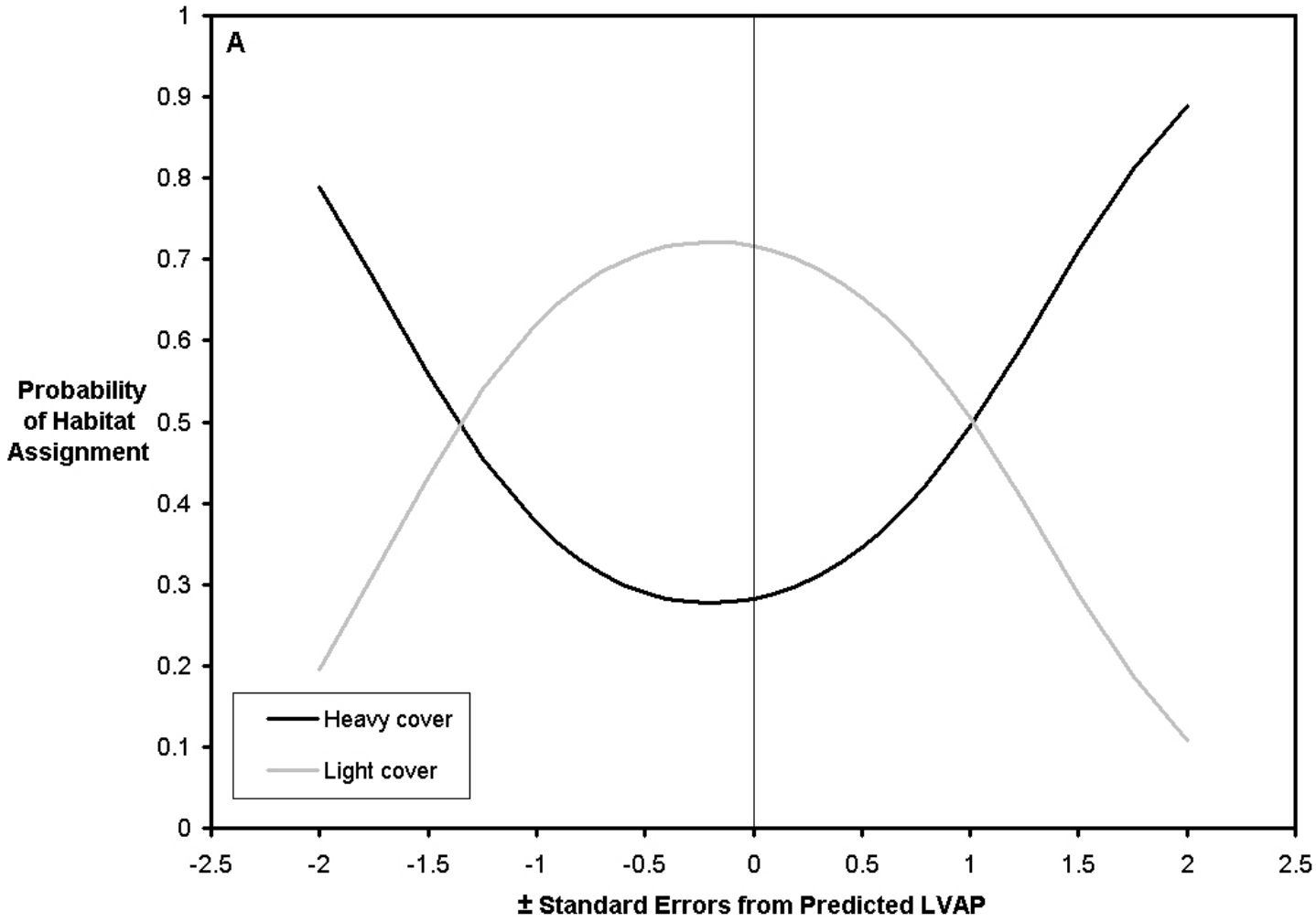


Figure 2.10: Effect of estimation of LVAP and MGSV on habitat classification of IPS CLL 20603. A, estimation of LVAP; B, estimation of MGSV. Curves are plotted showing changes in the probability of light cover and heavy cover habitat classification as LVAP and MGSV vary ± 2.5 standard errors about their estimates.

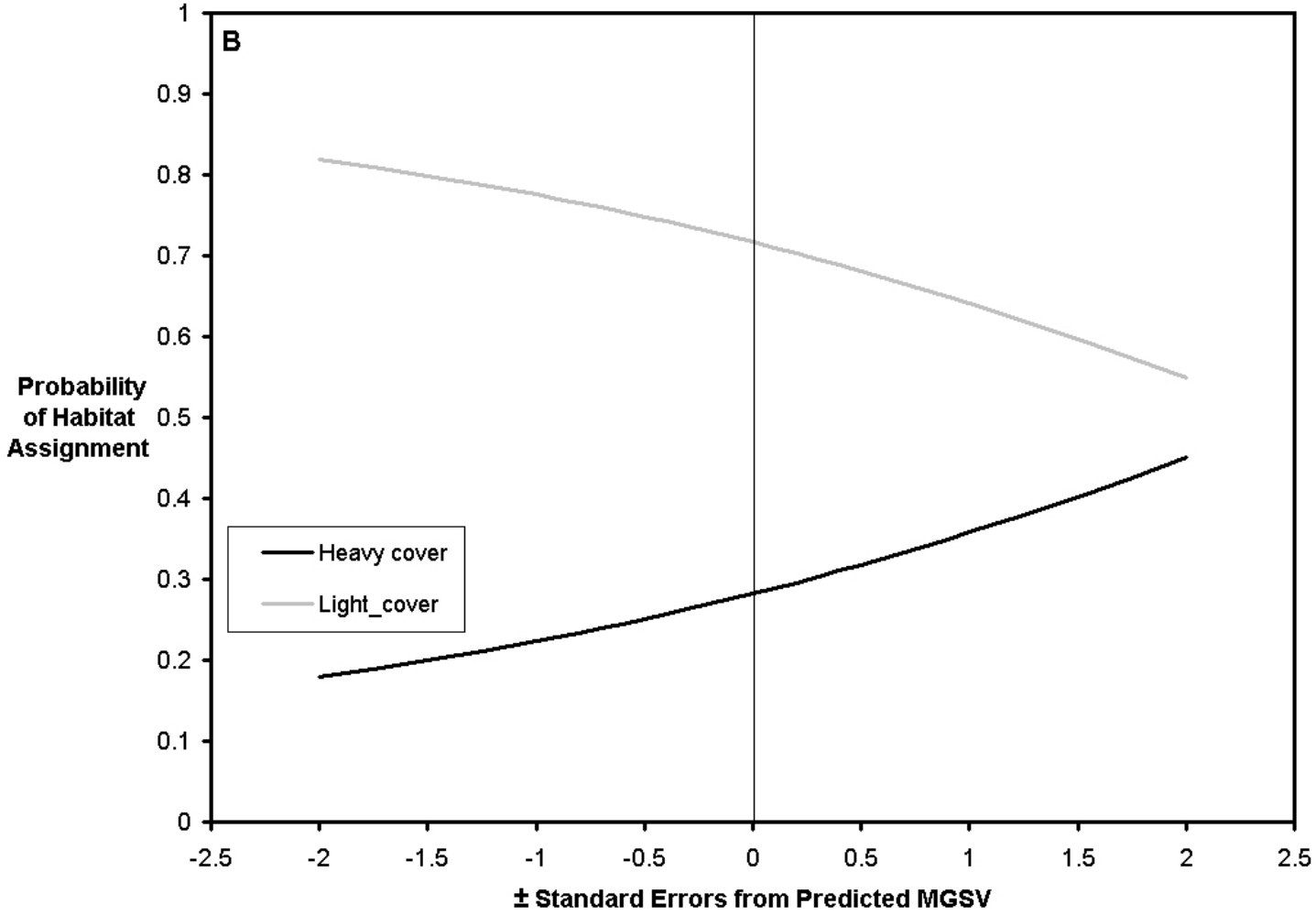


Figure 2.10: Effect of estimation of LVAP and MGSV on habitat classification of IPS CLL 20603. A, estimation of LVAP; B, estimation of MGSV. Curves are plotted showing changes in the probability of light cover and heavy cover habitat classification as LVAP and MGSV vary ± 2.5 standard errors about their estimates.

PART III: EQUID ECOMORPHOLOGY

Chapter 3: Introduction to Equid Ecomorphology

PROBLEMS AND ISSUES

The successful application of ecomorphology to the Bovidae for the purpose of reconstructing paleoenvironments relevant to hominid and hominoid evolution (e.g. Kappelman, 1991; Plummer & Bishop, 1994; Spencer, 1997; Scott et al., 1999) leaves open questions concerning what may be learned from other taxonomic groups common at relevant sites. In particular, following their immigration from the New World ca. 11.2 Ma to 10.7 Ma (Kappelman et al., 1996a; Kappelman et al., 1996b; Woodburne et al., 1996; Agusti et al., 1997; Sen, 1997; Agusti et al., 2001; Kappelman et al., 2003a; Scott et al., 2003) hipparionines are often a common faunal element at late Miocene sites (Alberdi et al., 1981; Alcalá, 1994; Barry et al., 2002; Scott et al., 2003). Thus, application of ecomorphology to hipparionines is an important component of understanding the composition of late Miocene faunas in Eurasia and is a needed complement to discussions of the paleoecology of these sites.

Hipparionines, however, pose a particularly difficult challenge in terms of ecomorphology. Much previous work has relied on a functional morphological framework first validated empirically using an extant comparative sample (see Kappelman, 1988; Spencer, 1995). In this respect, the Bovidae are ideal given both the wide range of habitat preferences and the taxonomic diversity of extant bovids (Kingdon, 1982; Estes, 1991). In contrast, the closest living relatives of tridactyl hipparionines are the much less diverse monodactyl equids. The range of habitats used by extant equids is small compared to those used by extant bovids making it more likely that extinct equids

occupied niches not known for extant equids. Moreover, the function of a tridactyl and monodactyl limb is certainly different. The evolutionary change from tridactyly to monodactyly is in fact often tied to environmental changes to drier and more open habitats (Camp & Smith, 1942; Sondaar, 1968). Thus, difficulties are posed for ecomorphological study of hipparionines both by the lower diversity and by the monodactyly of living equids.

Eisenmann (1995) following Gromova (1949; 1952) elaborated a functional framework for interpretation of hipparionine MP III's. Accordingly, MP III gracility was linked to open and/or dry environments. In part, the functional hypotheses linking gracility to open and dry habitats (Gromova, 1949; Gromova, 1952; Eisenmann, 1995) relies on a conceptualization of an evolutionary trajectory from tridactyly to functional monodactyly to monodactyly. Increasing MP III gracility is considered linked to a shift in the placement of the lateral metapodials from a lateral to a posterior-lateral position as the tridactyl foot becomes functionally more monodactyl. Primitive tridactyl forms are most tied to wet and forested habitats while modern monodactyl equids are more tied to dry and open environments. A tridactyl limb is thought to be advantageous in "…soft, sandy, or muddy soil in which this type of foot does not sink down so far." (Sondaar, 1968) or in habitats where obstructions are present (e.g., downed timber, brush) (Shotwell, 1961). The former hypothesis is in accord with observations of hipparionine trackways at Laetoli (Renders 1984). The accessory hooves appear to have contacted the ground during strides where one leg was slipping on the wet Laetoli ashfall. Thus, in this case, the function of accessory metatarsals may be linked to more or less frequent ground contact depending on substrate features (i.e. softness, sandiness, and muddiness). In contrast, monodactyly and the associated ligamental springing mechanism during locomotion are thought to

confer speed and endurance advantages in more open environments (Camp & Smith, 1942; Sondaar, 1968).

The structure of the metapodial diaphysis may also be linked to habitat due to the nature of bending moments generated by locomotion over different substrates (see Chapter 2). The difference in bending moments experienced by metapodials in dry and wet environments provides the functional hypothesis explaining the suggestion the mid-diaphysis dimensions are reduced in forms inhabiting drier habitats (Gromova, 1949; Gromova, 1952). Soft, uneven, or difficult substrates found in wet, rocky, or mountainous terrain leading to greater transverse bending would be expected to translate to greater medial-lateral diaphyseal diameters (Swartz, 1993).

Finally, elongate metapodials relative to body size or proximal limb segments have long been associated with cursorial locomotion (Gregory, 1912) and in turn linked to more open habitats (Scott, 1979; Scott, 1985). Functionally, relative distal limb elongation has been tied to considerations of both velocity and energetic efficiency (Hildebrand, 1985).

While the functional hypotheses noted above predict more gracile (and more specifically more slender and elongate) MP III's for dry and/or open habitats the range of habitat preferences and restriction to monodactyly for extant equids provides an empirically inadequate sample for the full validation of these hypotheses. In contrast, fossil hipparionines appear potentially quite diverse and may have ranged across more habitat types. The approach used here is necessarily more inductive than that used in past study of bovids and includes four parts. These are:

1) comparison across hipparionine metapodials and description of relative differences in theoretically interesting MP III morphology,

2) comparison of less well-understood fossil samples to well-studied samples of single populations with better understood habitat preferences (e.g., the Höwenegg hipparion: This work would have been impossible without the well-founded framework made possible by the extraordinary preservation of and body of scholarship on hipparions at the site of Höwenegg (Hegau, Germany) which creates the starting point for comparative work in this study.),

3) validation of functional hypotheses as much as possible with extant equid analogs, and

4) reference to a model developed using bovids based on the theoretically important dimensions of relative elongation and relative slenderness.

The analysis of Scott in Bernor et al. (2003b) showed the potential of using a comparative fossil sample to find likely relative differences in habitat between hipparion populations on the basis of MP III morphology (1 and 2 above). It appears that the fossil radiation of hipparionines can in fact serve as a comparative sample for supporting hypotheses regarding habitat-specific morphology. A principal components analysis of several standard equid metapodial metrics of specimens from a range of fossil sites including Xmas Quarry in North America, Höwenegg in Germany, Sinap in Turkey, and Rudabánya in Hungary was used to develop a metapodial taxonomy of these specimens. Principal components analysis is an exploratory data analysis technique that collapses multivariate data into a lesser number of correlated variables. These principal components have the advantage of showing potentially significant sets of morphological variation as well as clustering cases according to this variation. Most importantly, potential groupings of cases are generated with no *a priori* assumptions about group membership. If principal components replicate morphological gradients that are predicted to vary with habitat under a functional model, then they also serve to group specimens by

their relative position along a habitat gradient. Thus, a postcranial classification based on principal components can be a habitat-preference classification.

The findings of Bernor et al. (2003b) were that:

1) The first two principal components corresponded to morphology predicted to vary with habitat based on functional hypotheses: relative length and relative slenderness (or depth) (see Table 11.14 and 11.16 in Bernor et al., 2003b). This suggests that major components of MP III morphology are in fact related to function and habitat; that they are potential ecomorphological variables. It follows that differences between samples in these morphological components reflect difference in habitat. Comparison across hipparionine metapodials and description of relative differences in theoretically interesting MP III morphology should illuminate relative differences in habitat.
2) Based on the first component, the Höwenegg sample of metapodials appeared to be relatively short (compared to the other hipparionine metapodials in the sample) which would suggest less cursorial locomotion. Less cursorial species are predicted for more forested habitats. Such species may also have a relatively broad metapodial diaphysis (Eisenmann, 1995) and thus the scores for the second orthogonal (and hence independent) component of the Höwenegg sample were predicted to indicate a relatively broad diaphysis. The actual scores on principal component two for the Höwenegg sample confirm this. Furthermore, these data are consistent with the previous interpretations of the Höwenegg hipparionines as forest dwellers (Bernor et al., 1997). Moreover, the Höwenegg population formed a cluster as expected for a single species with a specific niche. Thus, use of the Höwenegg sample may be used

as a robust comparative standard for interpretation of paleohabitat on the basis of MP III morphology.

There are ecological differences among extant equids and these are discussed in greater depth in Chapter 5. For instance, both *Equus burchelli* GRAY, 1824 and *Equus grevyi* OUSTALET, 1882 are tied to open habitats. However, *Equus grevyi* is more constrained to arid and very open habitats (Estes 1991). In contrast, *Equus burchelli* is more like a light cover bovid (sensu Kappelman et al., 1997) using open woodlands and requiring wetter habitats (Estes 1991). Reconstructions based on hipparionine morphology will be strengthened inasmuch as the underlying functional basis of these reconstructions can be confirmed in the case of extant equids. This issue is discussed in Chapter 5.

The fourth part of the approach to equid ecomorphology used here involves the development of an empirical model applicable to equids based on bovids where habitat preferences are known and more variable. The generation of this empirical model was restricted to morphology found to be relevant to habitat for bovids in Chapter 2 that appears broadly analogous in equids. Thus, the morphology of bovid distal metapodials was excluded from consideration here. The result of this was a *habitat score* based on relative elongation and relative slenderness applicable to bovids, extant equines, hipparionines and potentially extendable to other taxa. The habitat score is intended as a heuristic for recognizing difference in habitat along a gradient from more open and dry to more closed and wet.

HABITAT SCORE

The combination of previous principal components analyses on hipparionines (Bernor et al., 1999; Bernor et al., 2003b; Kaiser et al., 2003; Scott & Maga, in press) and discriminant analyses on bovids (see Chapter 2) suggests that habitat cover may be

modeled as a continuous variable derived from morphological variables of the metapodial. Such a variable would be an extremely valuable heuristic for paleontologists and would work much like a hypsodonty index (Janis, 1988). As part of the quantification of hipparionine locomotor adaptation and likely habitat preference, such a variable is proposed and applied in this study. The goal for this habitat score is that it should have the following properties: 1) it should separate bovids of known habitats; 2) it should separate equines of known habitats; 3) it should separate fossil hipparionines where robust habitat interpretations have already been made; 4) the separation of forms from different habitats should occur in conformity with the biomechanical predictions made regarding morphology and habitat; and 5) the separation of bovids, hipparionines, and equines by habitat should be such that if closed habitat bovids have low scores relative to open habitat bovids then more closed habitat hipparionines should have low scores relative to more open habitat hipparionines. Closed habitat bovids need not necessarily have equivalent scores to closed habitat hipparionines but within taxonomic groups the trend from open to closed habitat should always be in the same direction as it is for other taxonomic groups.

Chapter 4: Materials and Methods

Ten standard metapodial measurements described by Eisenmann et al. (1988) and Bernor et al. (1997) were taken on metapodial III's (MP III's) belonging to a large sample of fossil hipparionines and a sample of extant species' of *Equus*. The measurements taken were M1, M3, M4, M5, M6, M10, M11, M12, M13 and M14. These measurements are relatively simple and were well diagrammed by Eisenmann et al. (1988).

The hipparionine sample measured here includes 217 complete metacarpal III's (hereafter MC III's) and 290 complete metatarsal III's (MT III's). MP III specimens were considered complete when all ten measurements were available for the specimen. Measurements were taken by the author primarily in the fall of 2001. Additional measurements were made available courtesy of Ray Bernor and some measurements were available in the literature. The measurements used here were standardized for the explicit purpose of allowing comparisons of measurements taken by different researchers and minimizing the impact of interobserver errors (Eisenmann et al., 1988).

Complete hipparionine metapodial III's were measured from 52 localities and17 countries. These are: Afghanistan (Molayan), Algeria (Bou Hanifia), Austria (Gols, Inzersdorf, Prottes, and Schwechat), France (Mt. Luberon), Germany (Dorn-Dürkheim, Eppelsheim, Esselborn, and Höwenegg), Greece (Maramena, Pikermi, Ravin de la Pluie, Saloniki, and Samos), Hungary (Baltavar, Csákvár, Kislang, Polgárdi, Sümeg), Pakistan (Siwaliks), Iran (Maragheh), Italy (Bacinello), Kazakhstan (Kalmakpai), Kenya (Lothagam), Libya (Sahabi), Spain (Ballestar, Can Llobateres, Concud, El Lugarejo, La Gloria 4, La Roma 2, La Tarumba/Villadecavalls, Layna, Los Valles de Fuentidueña, Piera, Polinya, Santiga, and Venta del Moro), Switzerland (Charmoille), Turkey

(Akkaşdağı, Çalta, Esme Akçaköy, and Sinap), and the USA (Christmas Quarry and Niobrara River). Incomplete metapodial III's where the M1 measurement (maximum length) was preserved were available from Nombrevilla and Can Ponsic in Spain and from Rudabánya in Hungary. These specimens were retained for some analyses.

The sample of *Equus* metapodials analyzed here includes 78 MC III's and 83 MT III's. The composition of the *Equus* sample is shown in Table BX.5. All of these measurements were taken by the author.

Previous studies (Bernor et al., 1999; Bernor & Scott, 2003; Scott & Maga, in press) have noted that description of hipparionine metapodials can be confounded by issues of scaling and concluded that a proxy measure for body size was necessary to understand the scaling of key morphological axes such as relative elongation and relative slenderness. Jungers et al. (1995) recommended geometric means as size variables in morphometric studies while K. Scott (1990) used non-length variables of metapodials to estimate equid body masses. Bernor and Scott (2003) note that the regression formulae of K. Scott (1990) tend to give differing body mass estimates based on MC III's and MT III's. Gordon (2002; 2003) argued that geometric mean size variables termed Global Size Variables (GSV's) are more stable measures of general body size than body mass estimates and can be measured without prediction errors. In Chapter 2, a GSV of non-length metapodial dimensions (Metapodial Global Size Variable or MGSV) was used to investigate the scaling of bovid metapodials. This bovid MGSV is precisely analogous to the geometric mean of nine non-length metapodial dimensions used by Bernor and Scott (2003) which they termed "GEOMEAN Size." Here, the same geometric mean size variable is used and will be referred to as MGSV (for consistency with Chapter 2). MGSV is calculated as follows:

MGSV = (M3 x M4 x M5 x M6 x M10 x M11 x M12 x M13 x M14)$^{(1/9)}$ The use of analogous size variables for equids and bovids facilitates the comparison of morphological trends associated with habitat preference in these two families and is necessary for any discussion of general morphological trends associated with habitat.

To understand the relationship between morphology and habitat independent of body size, all ten measurements were transformed to be independent of body size. This allows statements to be made concerning morphology such as relative elongation and relative slenderness. The transformation employed here is a refined version of the transformation used by Bernor & Scott (2003) and is also employed for bovids in Chapter 2.

Ratio measures of shape are often correlated with body size and may be driven by either the denominator or numerator. This complicates interpretations of shape differences among taxa. For instance, the measurement of diaphyseal shape with a ratio of M3:M4 may be 1) correlated with body size, and 2) could be driven by M3, M4 or both. Therefore, summarizing relative dimensions with a ratio of a measurement to a linear measure of body size (e.g., M3:MGSV) is preferred. Thus, in the case of diaphysis shape, the contributions of M3 and M4 may be isolated.

To account for shape differences driven by scaling, tests for correlation between ratio measurements and body size may be performed. Cases where ratios remain correlated with body size can be transformed to variables uncorrelated with body size by calculating residuals. We followed this procedure here.

To generate shape variables uncorrelated with body size and to thus summarize shape differences that are not the result of scaling, all ten measurements used in this study were first divided by MGSV and the resulting ratios were logged. These ratios were tested for a correlation with the log of MGSV using the entire hipparionine sample in

SAS (SAS Institute, Cary, NC). In cases where a significant correlation was found ($p < 0.05$) the residual of the logged ratios was computed. This residual is identical to the residual of the logged measurement versus the log of MGSV.[3] The result was ten variables uncorrelated with MGSV that were either the log of a simple ratio or the residual of that simple ratio. Each of these variables was designated with the prefix "si" for "size independent."

Previous principal components analyses (PCA) of Sümeg (Bernor et al., 1999), Sinap (Bernor et al., 2003b), Dorn-Dürkheim (Kaiser et al., 2003), and Akkaşdağı (Scott & Maga, in press) have successfully sorted hipparionine MP III's into biologically significant groups. Accordingly, I conducted PCA's of hipparionine MT III's and MC III's in SAS using all ten size independent variables (siM1, siM3, siM4, siM5, siM6, siM10, siM11, siM12, siM13, siM14). The resulting principal components reflect total variation in metapodial shape for the sample considered here. Inspection of PCA plots is a powerful heuristic for identifying clusters of similarly shaped metapodials and the eigenvectors for specific components can be interpreted with respect to *a priori* predictions regarding possible morphological associations with habitat.

The Höwenegg (Germany) sample has been used in the past as an analytical standard for the interpretation of PCA's (Bernor et al., 1999; Bernor & Scott, 2003; Bernor et al., 2003b; Kaiser et al., 2003; Scott & Maga, in press) because it is well-sampled and from a single species and a single site. In this study, Höwenegg is again used as an analytical standard. Following Scott and Maga (in press), a second sample of Vallesian MP III's from La Roma 2 (Spain) was added as an additional standard. Like the Höwenegg sample, the La Roma 2 sample appears to include only a single species. La

[3] For example, the residual of $\log_{10}(M1/MGSV)$ regressed against of $\log_{10}(MGSV)$ is identical to the residual of $\log_{10}(M1)$ regressed against of $\log_{10}(MGSV)$ because $\log_{10}(M1/MGSV) = \log_{10}(M1) - \log_{10}(MGSV)$.

Roma 2 is also better sampled than most hipparionine localities (16 complete MT III's and 7 complete MC III's).

To derive a general habitat score linking metapodial morphology and habitat, an empirical approach was adopted to create a linear combination of variables reflecting habitat variability within bovids, equines, and hipparionines. Since the extant bovid radiation encompasses species with known and divergent habitat preferences, a bovid model was used to generate such a linear combination of variables. The bovid analogs of the variables siM1 and siM3, rcMLEN and rcMML, appear strongly associated with habitat and these variables are likely the best hipparionine habitat indicators as well (see Chapter 2). Therefore, siM1 and siM3 were chosen as the morphological basis for a "habitat score."

A canonical variable was derived using SAS based on bovid analogs of siM1 and siM3 for those bovids categorized in the plains and forest habitat groups. Canonical variables are similar to principal components with the key distinction that they summarize between group variance and can only be applied in cases where group membership is known. Thus, canonical variables can be computed for bovids of known habitat. The coefficients of these canonical variables may potentially be applicable to other taxa where precisely analogous variables are known. This appears likely in the case of bovids and equids.

The canonical variable based on siM1 and siM3 maximizes the variance explained between plains and forest bovids (as classified in Chapter 2). This canonical variable is potentially a valuable habitat indicator for bovids and is used as the basis of a habitat score (HS). The coefficients by which siM1 and siM3 were multiplied to determine HS for bovids were then applied to siM1 and siM3 for hipparionine and equine

specimens. The resulting scores can be evaluated with respect to the criteria outlined in Chapter 3 for an appropriate and heuristic habitat score.

Chapter 5: Extant Equidae

RESULTS

Size independent variable computation

For MT III's, the logged ratios of M1 and M13 over MGSV were significantly correlated with $\log_{10}$(MGSV) ($p < 0.01$, see tab. 5.1) and residuals were computed for these ratios. These residuals were adopted as size independent shape variables and are referred to as siM1 and siM13 respectively. The logged ratios for M3, M4, M5, M6, M10, M11, M12 and M14 over MGSV were not significantly correlated with MGSV (tab. 5.1) and these ratios were retained for the remainder of the MT III analysis. They are referred to as siM3, siM4, siM5, siM6, siM10, siM11, siM12, and siM14.

In the case of MC III's, only the logged ratios of M1 and M6 over MGSV were significantly correlated with $\log_{10}$(MGSV) ($p <0.01$, see tab. 5.1). Thus, residuals were used for siM1 and siM6 and the logged ratios for M3, M4, M5, M10, M11, M12, M13 and M14 over MGSV were used for siM3, siM4, siM5, siM10, siM11, siM12, siM13 and siM14.

Principal components analysis

While principal components analysis (PCA) will yield principal components equal to the number of variables in the analysis, each additional component explains a smaller proportion of the sample variance and is likely of diminished importance. Accordingly, Scott and Maga (in press) limited discussion to components that explained at least 10% of the sample variance. This rule was applied here to the PCA's of living equine MP III's.

Metatarsal III

PCA of extant equid MT III's (N = 83) resulted in four principal components that each accounted for greater than 10% of the total variance. Cumulatively, these four components explained 81.1% of the variance (tab. 5.2). Of these four components, principal component one (PC1) explained 37.29% of the variance and summarized variability mainly in siM1 and to a lesser extent siM5 (tab. 5.3). Increased scores on PC1 corresponded to increased length relative to size as indicated by a positive eigenvector of 0.777 with siM1 and to a decreased medial-lateral dimension of the proximal articular surface as indicated by a negative eigenvector of -0.484 (tab. 5.3). It would appear that PC1 largely summarizes relative MT III elongation.

PC2 for extant equid MT III's expresses general diaphyseal robusticity and explained 18.41% of the variance (tab. 5.2). PC2 appears highest when values siM3 and siM4 are relatively great as indicated by positive eigenvectors with siM3 and siM4 of 0.542 and 0.583 respectively (tab. 5.3). Thus, PC2 identifies forms with a robust MT III diaphysis.

PC3 explains 15.14% of the variance and appears to mostly express the relative expansion of the medial-lateral dimension of the proximal articular surface. It had a positive eigenvector of 0.716 with siM5. PC4 explained 10.26% of the variance and had a strong negative eigenvector (= -0.713) with the anterior-posterior dimension of the articular surface, siM5. Thus, together PC3 and PC4 summarize variation in the distribution of the proximal articular surface.

Metacarpal III

Principal components analysis (PCA) of the sample of 78 extant equid MC III's yielded a result similar to that for the PCA of MT III's. PC1 explained 39.18% of the

variance (tab. 5.2) and had a positive eigenvector of 0.826 with relative length, siM1 (tab. 5.3). Thus, as in the case of the MT III, PC1 appears to express relative elongation.

PC2 explained 17.91% of the variance in the MC III sample (tab. 5.2) and had a strong negative eigenvector (= -0.579) with siM4 (tab. 5.3). Thus, PC2 appears to express the anterior-posterior reduction of the diaphysis.

PC3 explained 12.83% of the MC III sample variance (tab. 5.2). PC3 had the strongest eigenvectors with to medial-lateral variables, siM3 (0.481) and siM5 (-0.620) (tab. 5.3). Thus, the morphological trend expressed is one of medial lateral expansion of the diaphysis and reduction of the medial-lateral proximal articular surface.

PC4 explained 11.34% of the variance (tab. 5.2) and had a very strong positive eigenvector of 0.829 with siM10 (tab. 5.3). Thus, PC4 appears to largely express the relative expansion of the distal supra-articular breadth.

Habitat score computation

One significant canonical correlation each was generated for bovid and antilocaprid metatarsals and metacarpals assigned to either the plains or forest habitat groups ($p<0.0001$) based on the variables rcMLEN and rcMML. The resulting canonical variables maximized the separation between the forest and plains groups on the basis of rcMLEN and rcMML. These canonical variables can be considered as possible habitat scores.

The equations generated by the canonical analysis for the computation of habitat scores (HS) are as follows:

Metatarsal HS = (7.596 x rcMLEN) + (-30.063 x rcMML)

Metacarpal HS = (3.718 x rcMLEN) + (-30.494 x rcMML)

Forest bovids have negative habitat scores while plains habitat bovids have positive habitat scores in the case of both metacarpals and metatarsals. Similarly,

intermediate habitat bovids which were not part of the sample used to determine the habitat score coefficients appear to differ in terms of habitat score according to the same trend. Heavy cover habitat bovids had a lower mean habitat score than light cover bovids. Mountain forms had lower mean habitat scores than forest forms. In the case of the metatarsals, these differences were significant ($p < .05$, Kruskal-Wallis test). These differences in habitat score can be seen in figure 5.1 where mean habitat scores are shown for each habitat and for selected living equids.

The equations used to calculate habitat score for the bovid/antilocaprid sample were applied to the living equid sample. The analogous extant equid variables siM1 and siM3 were substituted for rcMLEN and rcMML. Since the logged ratio of M3 to MGSV was not significantly correlated with the $\log_{10}$(MGSV) for extant equid MT III's and extant equine MC III's, it was used for siM3. Therefore, the siM3 was standardized to the mean in the case of living equid MC III's and MT III's. Thus, the habitat scores for extant equids were generated using the standardized values for siM3 and the variable siM1 which is a residual. This insures that the extant equid habitat scores were expressed in the same scale as the bovid habitat scores.

Thus, the habitat score for a specimen is a linear combination of variables summarizing metapodial length and metapodial diaphysis breadth relative to the scaling trend for the that specimen's taxonomic group. Large habitat scores for extant equid specimens correspond to metapodials that are slender and elongate compared to other extant equid specimens while large habitat scores for bovid specimens correspond to metapodials that are slender and elongate compared to other bovid specimens.

Principal components and habitat scores of selected extant equids

The extant equid sample evaluated here included a variety of species and specimens of various breeds of domestic horse. Results of PCA and habitat score

computations are presented for a selected subset of this sample. The total sample was considered superior for testing scaling relationships and determining principal components. However, discussion of trends in principal component scores and habitat scores is restricted to better sampled species with known habitat preferences. In the case of domestic horses, discussion is restricted to a group of specimens identified as Arabians which are well known for their speed and endurance. Results for the following groups are reported below: *Equus zebra*, *Equus burchelli*, *Equus grevyi*, *Equus hemionus*, and *Equus caballus* (Arabian).

Habitat score

The living equids were separated according to habitat score. In the case of the MT III, this separation was most marked (fig. 5.1A). Mean habitat scores based on MT III's increased from *Equus zebra* to *Equus burchelli* to *Equus grevyi* to *Equus hemionus* to the Arabian breed of *Equus caballus*. The distinction between *Equus burchelli* and *Equus grevyi* was most distinct and the mean habitat scores for these two species did not overlap at the 95% confidence level.

The same general trend in habitat score was evident for MC III's but was much less marked (fig. 5.1B). MC III mean habitat score was again lowest for *Equus zebra* followed by *Equus burchelli* and then *Equus grevyi* and the Arabian which had nearly identical mean habitat scores. *Equus hemionus* had the greatest mean habitat score based on MC III's.

Principal component one

Equus burchelli, *Equus grevyi*, and *Equus hemionus* are all clearly distinguished by PC1 which expresses MP III elongation. This is true for both MT III's and MC III's (fig. 5.2). *Equus burchelli* appears to have the least elongate MP III's of these three

species while *Equus hemionus* has the most elongate MP III's. *Equus grevyi* is intermediate between *Equus burchelli* and *Equus hemionus* on PC1. *Equus zebra* would appear to have the relatively shortest MP III's but the sample of size for *Equus zebra* was small. The Arabian had scores for PC1 that were similar to those for *Equus grevyi* in the case of MT III's and similar to *Equus burchelli* in the case of MC III's.

Principal component two

PC2 expressed general diaphysis robusticity in the case of MT III's while in the case of MC III's it appears to mainly express the anterior-posterior reduction of the diaphysis. There was little distinction between equid species as far as MT III diaphysis robusticity. The Arabian and *Equus hemionus* appeared perhaps slightly less robust but the trend was not strong (fig. 5.3A).

PC2 for the equid MC III's resulted in a more clear distinction between the Arabian and *Equus hemionus* on the one hand and the three zebra species on the other hand (fig. 5.3B). The Arabian and *Equus hemionus* had elevated scores for PC2 which indicated a reduction in the anterior-posterior dimension of the diaphysis accompanied by a lesser reduction in the medial-lateral dimension of the diaphysis.

Principal component three

PC3 for MT III's expressing the medial-lateral expansion of the proximal articular surface distinguished the Arabian, *Equus grevyi*, and *Equus hemionus* with positive scores for PC3 from *Equus burchelli* and *Equus zebra* with negative scores for PC3 (fig. 5.4A).

MC III's displayed the opposite trend. PC3 for MC III's expressed the medial-lateral reduction of the proximal articular surface and the concomitant expansion of the medial-lateral dimension of the diaphysis. MC III's of the Arabian had maximal values

for PC3 and MC III's of *Equus zebra* and *Equus burchelli* had minimum values for PC3 (fig. 5.4B).

Principal component four

Equus burchelli and even more so *Equus grevyi* appear to have expanded MT III proximal articular surfaces as indicated by low scores for PC4 (fig. 5.5A). The only case of a strong loading of a distal MP III variable with a major principal component in the extant equid analysis was the case of siM10 and PC4 in the MC III analysis. PC4 appears to express relative expansion of the MC III distal supra-articular breadth and was most elevated for *Equus burchelli* and to a much lesser extent the Arabian (fig. 5.5B).

DISCUSSION

Relative elongation and relative slenderness

One notable result of the PCA's of living equid MP III's was that the variable siM3 was not strongly associated with any of the major principal components in a way that unambiguously expressed relative diaphysis slenderness. For example, while siM3 loaded strongly and positively with PC2 in the MT III analysis, siM4 had an even stronger positive loading. Thus, in this case, PC2 expressed general diaphysis robusticity as opposed to some measure of relative diaphysis slenderness. This result contrasts with the predominant role of siM3 in separating bovids of different habitats and previous results (Scott & Maga, in press) implicating it as an important variable distinguishing different hipparionines. However, siM3 is given the strongest weight in the calculation of habitat score and the resulting habitat scores for living equids provide a robust separation of species (especially in the case of MT III's) (fig. 5.1).

To further describe the variability in relative slenderness for living equids, siM3 and siM1 have been plotted in figure 5.6. In the case of both MT III's and MC III's, the

living equids appear to be distinguished mainly by siM1. However, siM3 appears to play a role nonetheless. In the case of MT III's, *Equus burchelli* commonly has elevated values for siM3 while *Equus grevyi* and *Equus hemionus* have lower values for siM3 indicating in general greater slenderness. For MC III's, values for siM3 appear to decline from *Equus burchelli* to *Equus grevyi* to *Equus hemionus*.

The contrast between *Equus burchelli* and *Equus grevyi* confirms hypotheses regarding habitat and MP III morphology. Both *Equus burchelli* and *Equus grevyi* are linked with open habitats. However, *Equus grevyi* is more constrained to arid and very open habitats (Estes, 1991) whereas *Equus burchelli* is more like a light cover bovid using open woodlands and requiring wetter habitats (Estes, 1991). The distinction between *Equus grevyi* and *Equus burchelli* in siM3 supports the hypothesis that mid-diaphysis dimensions are reduced in forms inhabiting drier habitats (Gromova, 1949; Gromova, 1952). *Equus zebra* which frequents rocky, barren uplands (Estes, 1991) also had higher values for siM3. This supports the more general idea that soft, uneven, or difficult substrates found in wet, rocky (as in the case of *Equus zebra*), or mountainous terrain leading to greater transverse bending would be expected to translate to greater medial-lateral diaphyseal diameters.

Equus hemionus in this study includes specimens assigned to various subspecies (e.g.. *Equus hemionus hemionus* and *Equus hemionus kiang*). Most of the specimens measured here come from Mongolia and *Equus hemionus* can be considered an inhabitant mainly of dry, open steppe country (i.e., the kiang-steppe of broad plains with xerophyllous vegetation interspersed with swampy valleys of Groves, 1974). Thus, the elongate and slender MP III's of *Equus hemionus* (fig. 5.2 & 5.6) are associated with a generally dry and open habitat.

The summary plots of principal components one through four (figs. 5.2-5) indicate that relative length is preeminent in distinguishing the living equid species analyzed here. PC1 (=relative elongation) not only explains the most variance of the four principal components, it also best distinguishes equids by species. Moreover, the trend in relative elongation is as expected based on habitat use.

Habitat score validity

The general trend noted above where equids using wetter habitats and more woodland areas are associated with shorter and broader MP III's while equids exploiting dry and open or steppe habitats have more elongate and slender metapodials translates into reduced habitat scores for *Equus burchelli* compared to *Equus grevyi* and *Equus hemionus*. Thus, habitat scores whose coefficients were determined using a bovid model successfully sort living equids by habitat. Moreover, the Arabian horse known for speed and endurance (Bongianni, 1988) also had increased habitat scores greater than those for *Equus burchelli*. Thus, the living equids have habitat scores that in relative terms conform to expectations based on their habitats and in the case of the Arabian expectations based on its cursorial reputation. Critically, *Equus zebra* and *Equus burchelli* have lower habitat scores while *Equus grevyi*, *Equus hemionus* and the Arabian have higher habitat scores. This pattern confirms that the habitat score weightings and variables selected based on a bovid analogy can successfully be applied to equids.

SUMMARY

PCA of living equids revealed the critical importance of differences in relative MP III elongation between extant equid species. Relative slenderness was not emphasized in the results of PCA of extant equids. However, siM3 (relative mid-diaphysis breadth) does vary by species in a manner as predicted by their habitat. In

combination, the degree of relative elongation and relative slenderness for MP III's of extant equids results in habitat scores that successfully sort living equids according to habitat. This result suggests that habitat scores based on a bovid analog can be used to sort equids by habitat.

Table 5.1: Least squares regression statistics for morphological variables versus size for extant Equidae.

Element	Variable*	Intercept	Slope	*df*	R^2	*P*	95% Confidence Interval of the Slope	95% Confidence Interval of the Intercept
MT3	M1	1.3602	-0.3176	81	0.2900	<0.0001	-0.4275 - -0.2077	1.1907- 1.5298
MT3	M3	-0.0589	-0.0083	81	0.0008	0.7992	-0.0728- 0.0562	-0.1585- 0.0406
MT3	M4	-0.1954	0.0666	81	0.0441	0.0569	-0.002- 0.1352	-0.3013 - -0.0896
MT3	M5	0.1044	0.0093	81	0.0005	0.8364	-0.0802- 0.0988	-0.0337- 0.2425
MT3	M6	0.0806	-0.0259	81	0.0067	0.4624	-0.0957- 0.0439	-0.027- 0.1883
MT3	M10	0.0697	0.0242	81	0.0098	0.3734	-0.0296-0.078	-0.0133- 0.1527
MT3	M11	0.0684	0.0179	81	0.0073	0.4426	-0.0283- 0.0641	-0.0028- 0.1396
MT3	M12	-0.0131	0.0102	81	0.0032	0.6142	-0.0299- 0.0503	-0.075- 0.0487
MT3	M13	-0.0375	-0.0609	81	0.1125	0.0019	-0.0986 - -0.0231	-0.0958- 0.0208
MT3	M14	-0.0181	-0.0332	81	0.0277	0.1329	-0.0768- 0.0103	-0.0853-0.049
MC3	M1	1.0807	-0.1697	76	0.1123	0.0027	-0.2787 - -0.0607	0.915- 1.2464
MC3	M3	-0.0630	0.0159	76	0.0044	0.5643	-0.0387- 0.0705	-0.146- 0.0201
MC3	M4	-0.2215	0.0529	76	0.0253	0.1639	-0.022- 0.1278	-0.3354 - -0.1076
MC3	M5	0.1113	0.0237	76	0.0079	0.4393	-0.0371- 0.0846	0.0188- 0.2037
MC3	M6	0.1952	-0.1595	76	0.3606	<0.0001	-0.208 - -0.1109	0.1215- 0.2689
MC3	M10	0.0576	0.0435	76	0.0229	0.1858	-0.0214- 0.1085	-0.0411- 0.1563
MC3	M11	0.1327	-0.0099	76	0.0019	0.7080	-0.062- 0.0423	0.0534- 0.2121
MC3	M12	-0.0502	0.0353	76	0.0276	0.1458	-0.0125- 0.0831	-0.1229- 0.0224
MC3	M13	-0.0931	-0.0093	76	0.0037	0.5970	-0.044- 0.0255	-0.1459 - -0.0403

MC3	M14	-0.0690	0.0073	76	0.0017	0.7204	-0.033- 0.0476	-0.1303 - - 0.0077

*Variables are the tabled measurement from Eisenmann (1988) divided by the size variable MGSV and logged. Regression statistics are for these variables regressed against $\log_{10}$(MGSV).

Table 5.2: Eigenvalues for Principal Components Analysis (PCA) of MT III and MC III of extant Equidae.

Element	Principal Component	Eigenvalue	% Variance Explained
MT III	One	0.00160465	37.29%
MT III	Two	0.00079236	18.41%
MT III	Three	0.00065176	15.14%
MT III	Four	0.00044157	10.26%
MT III	Five	0.00034378	7.99%
MT III	Six	0.00024727	5.75%
MT III	Seven	0.00011975	2.78%
MT III	Eight	0.00006985	1.62%
MT III	Nine	0.00003108	0.72%
MT III	Ten	0.00000167	0.04%
MC III	One	0.00127084	39.18%
MC III	Two	0.00058078	17.91%
MC III	Three	0.00041616	12.83%
MC III	Four	0.00036785	11.34%
MC III	Five	0.00019858	6.12%
MC III	Six	0.00016244	5.01%
MC III	Seven	0.00014381	4.43%
MC III	Eight	0.00005187	1.60%
MC III	Nine	0.00004132	1.27%
MC III	Ten	0.00000989	0.30%

Table 5.3: Eigenvectors for Principal Components Analysis (PCA) of MT III and MC III of extant Equidae.

		Eigenvector			
Element	**Variable**	**Principal Component One (PC1)**	**Principal Component Two (PC2)**	**Principal Component Three (PC3)**	**Principal Component Four (PC4)**
MT III	siM1	0.777	0.000	0.537	0.087
MT III	siM3	-0.154	0.542	0.121	-0.013
MT III	siM4	0.226	0.583	-0.051	-0.338
MT III	siM5	-0.484	-0.213	0.716	-0.204
MT III	siM6	0.188	-0.386	-0.309	-0.713
MT III	siM10	-0.068	0.173	-0.178	0.278
MT III	siM11	-0.031	-0.041	-0.213	0.291
MT III	siM12	0.051	-0.254	-0.072	0.265
MT III	siM13	0.078	-0.170	-0.051	0.242
MT III	siM14	0.194	-0.216	0.036	0.193
MC III	siM1	0.826	0.387	0.062	0.138
MC III	siM3	-0.085	-0.297	0.481	0.038
MC III	siM4	0.384	-0.579	0.292	0.092
MC III	siM5	0.015	-0.285	-0.620	-0.342
MC III	siM6	0.161	-0.105	-0.336	0.117
MC III	siM10	-0.206	0.157	-0.230	0.829
MC III	siM11	-0.235	0.199	0.292	-0.014
MC III	siM12	-0.138	0.377	0.193	-0.250
MC III	siM13	-0.028	0.235	0.011	-0.186
MC III	siM14	0.136	0.269	-0.080	-0.236

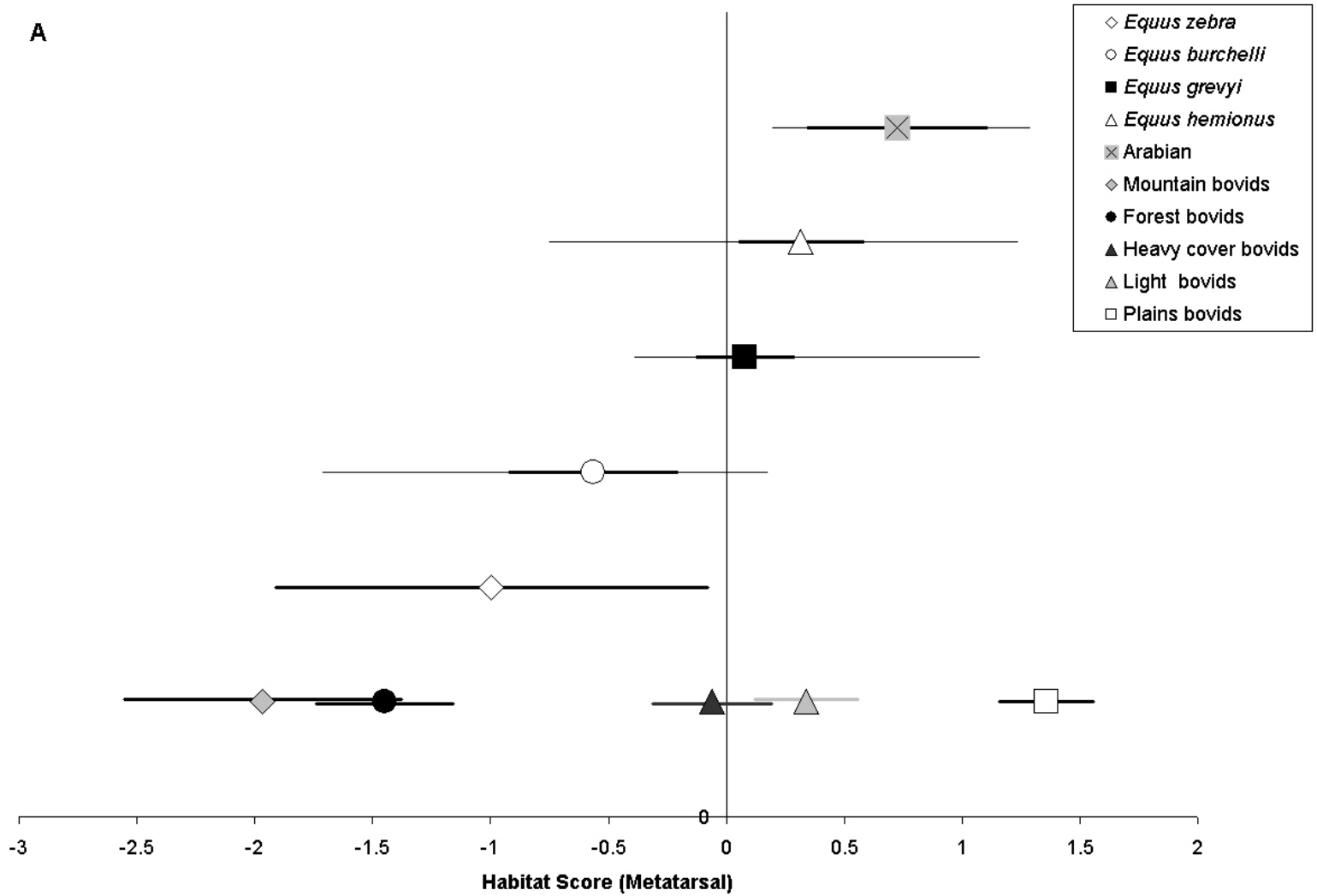


Figure 5.1: Summary of habitat scores for selected extant equids with bovid habitat scores by habitat category. A, metatarsals; B, metacarpals. The horizontal axis is habitat score (based on size, metapodial length, and metapodial width at midshaft). The 95% confidence intervals are denoted by thick lines and ranges are shown as thin lines.

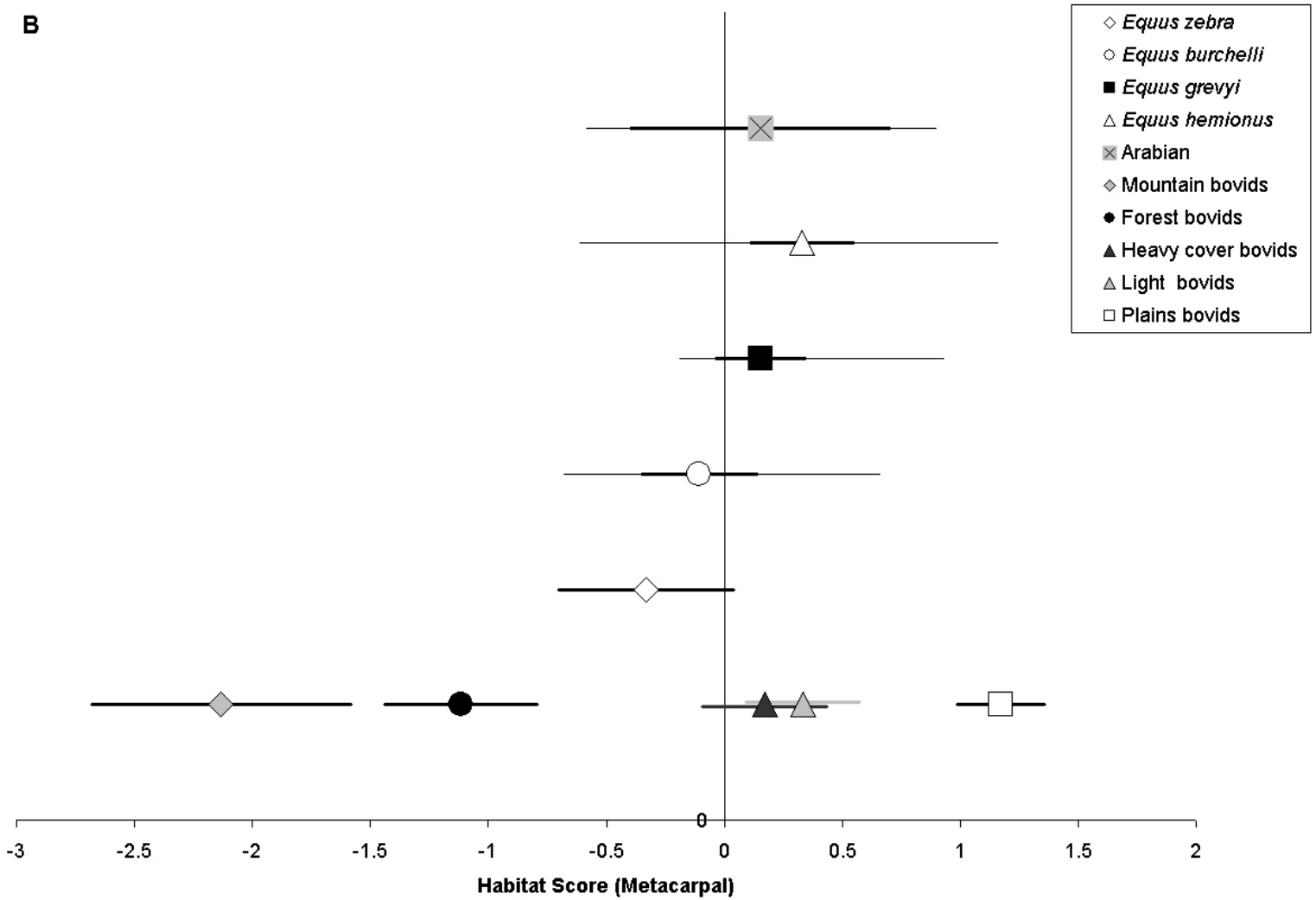


Figure 5.1: Summary of habitat scores for selected extant equids with bovid habitat scores by habitat category. A, metatarsals; B, metacarpals. The horizontal axis is habitat score (based on size, metapodial length, and metapodial width at midshaft). The 95% confidence intervals are denoted by thick lines and ranges are shown as thin lines.

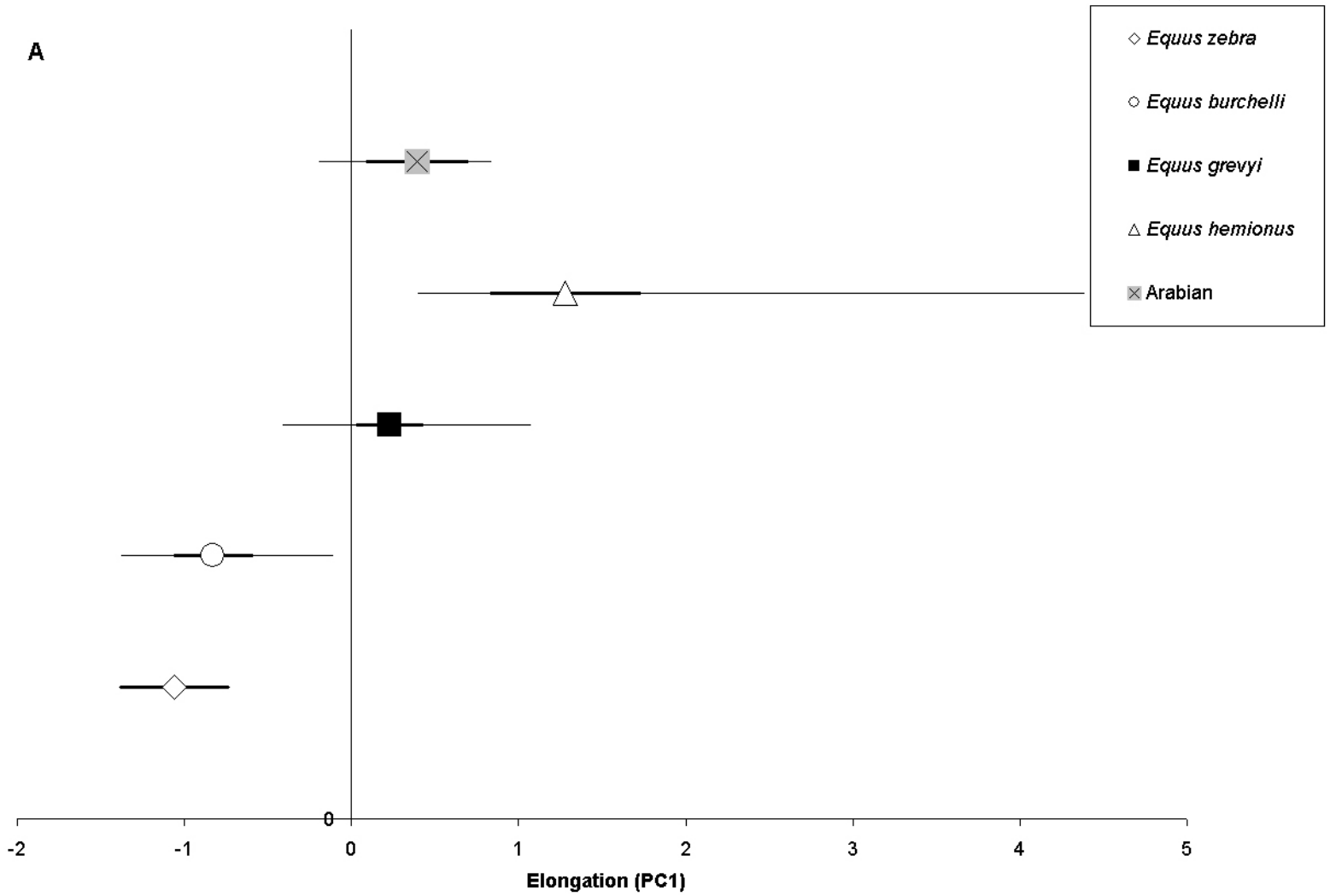


Figure 5.2: Summary plot of PC1 for extant equids. A, MT III's; B, MC III's. Mean principal component scores are shown with 95% confidence intervals denoted by thick lines and ranges shown as thin lines.

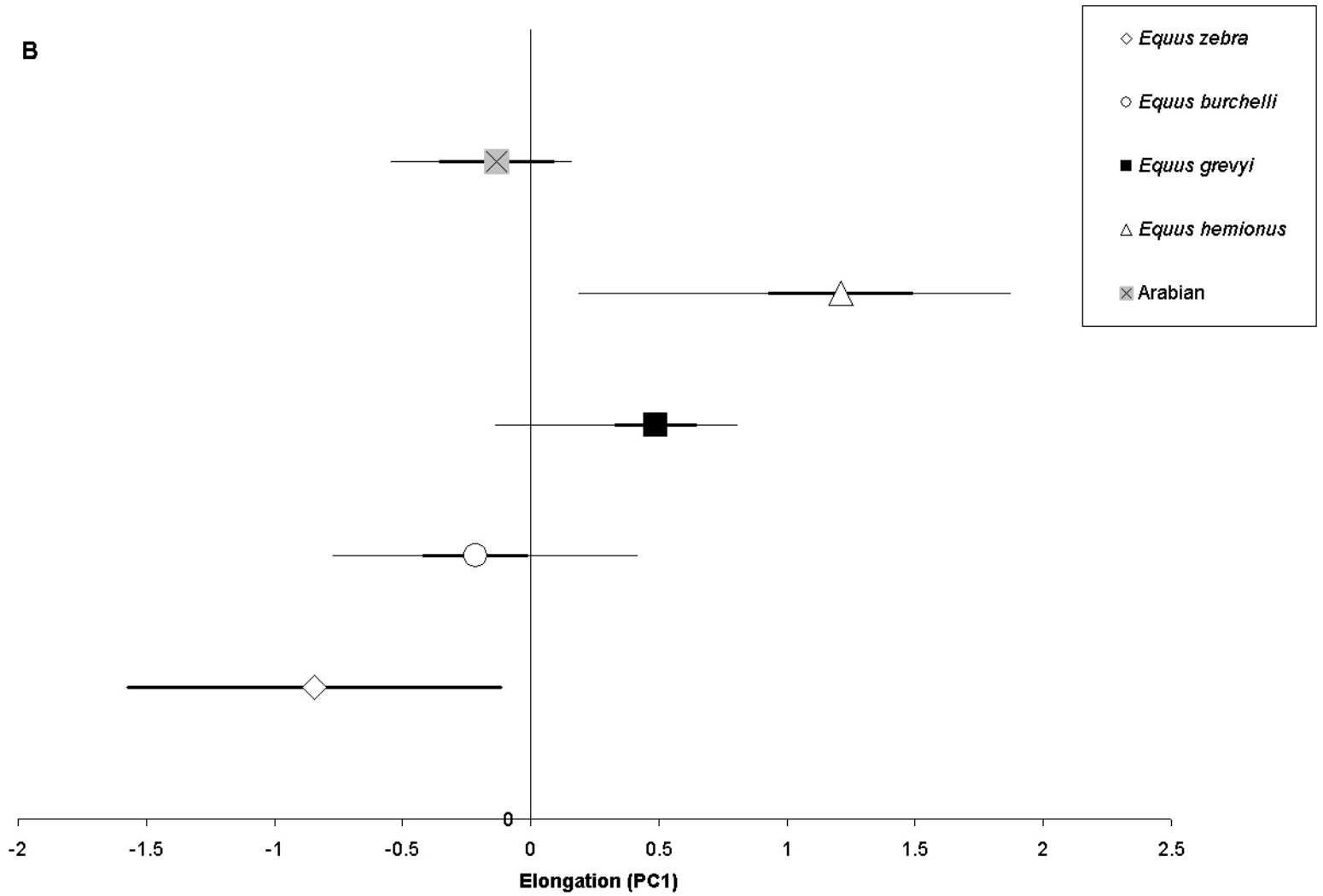


Figure 5.2: Summary plot of PC1 for extant equids. A, MT III's; B, MC III's. Mean principal component scores are shown with 95% confidence intervals denoted by thick lines and ranges shown as thin lines.

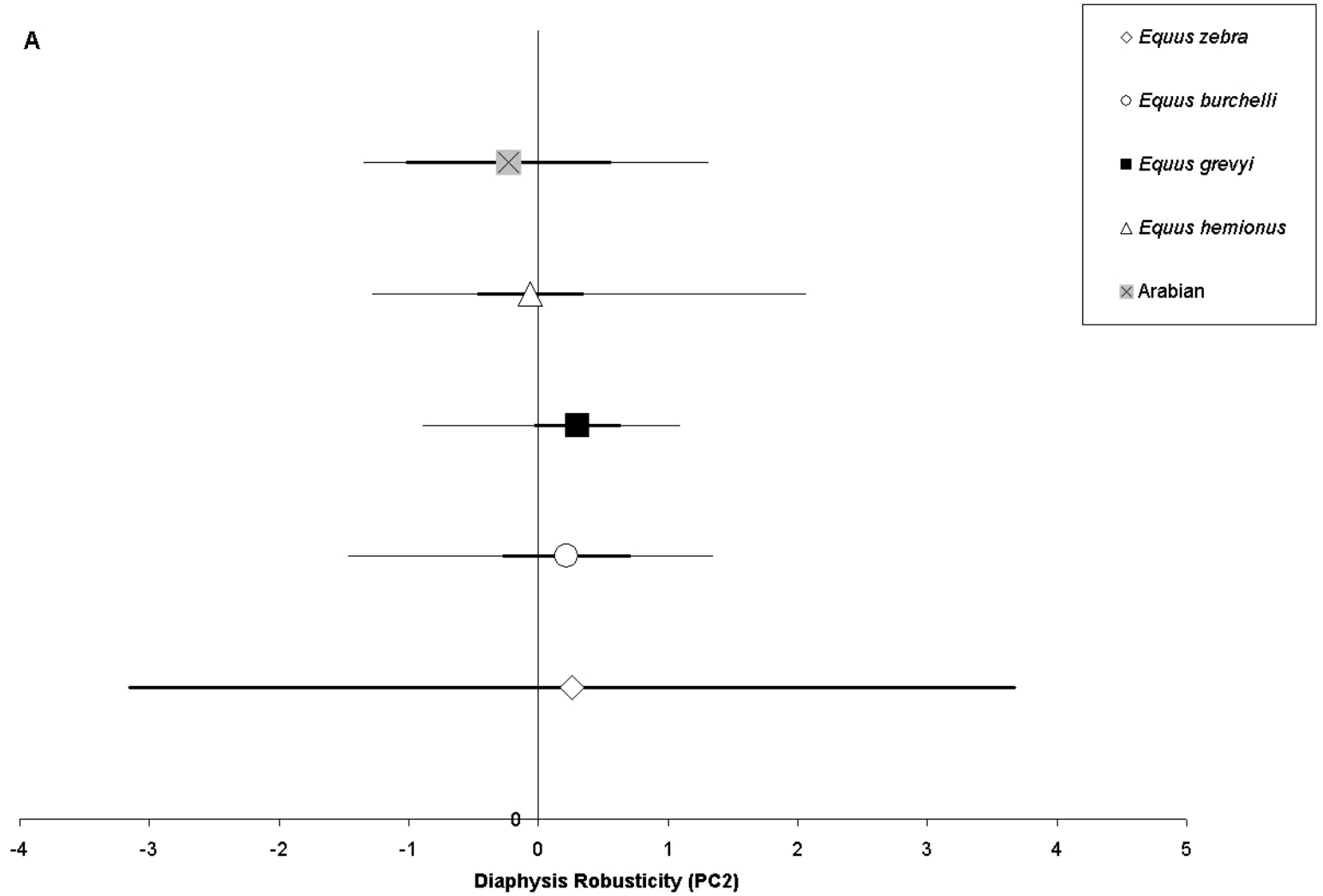


Figure 5.3: Summary plot of PC2 for extant equids. A, MT III's; B, MC III's. Mean principal component scores are shown with 95% confidence intervals denoted by thick lines and ranges shown as thin lines.

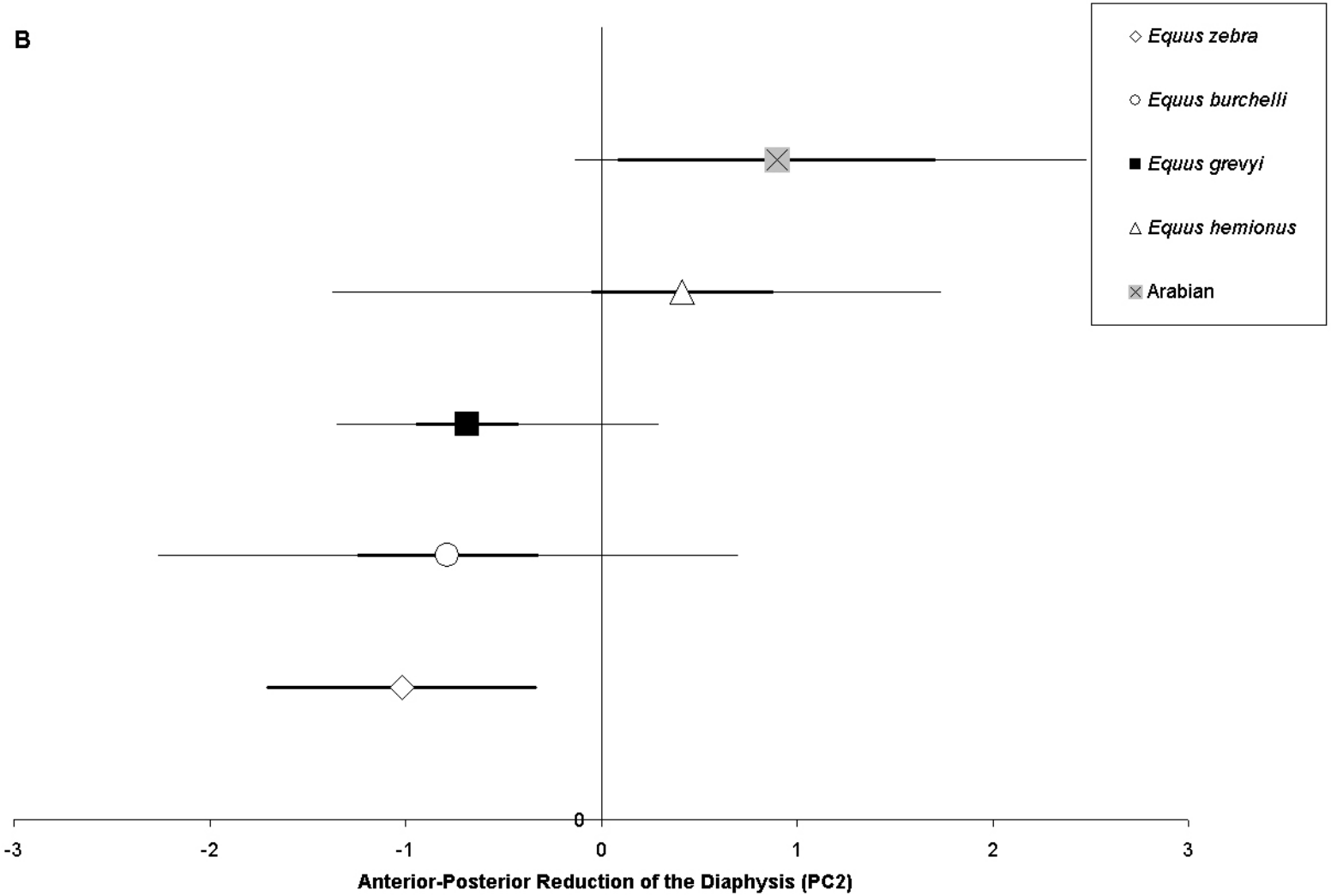


Figure 5.3: Summary plot of PC2 for extant equids. A, MT III's; B, MC III's. Mean principal component scores are shown with 95% confidence intervals denoted by thick lines and ranges shown as thin lines.

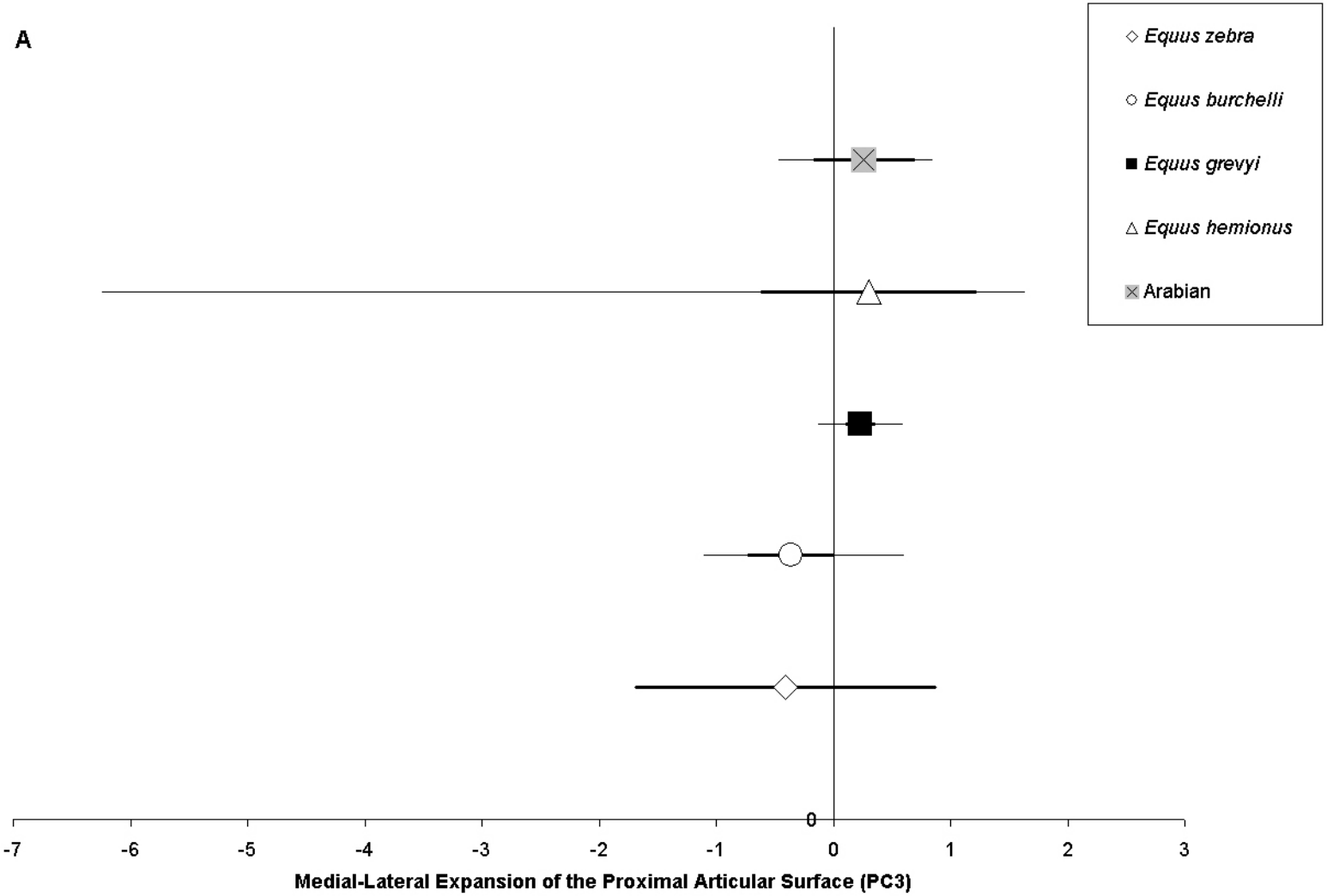


Figure 5.4: Summary plot of PC3 for extant equids. A, MT III's; B, MC III's. Mean principal component scores are shown with 95% confidence intervals denoted by thick lines and ranges shown as thin lines.

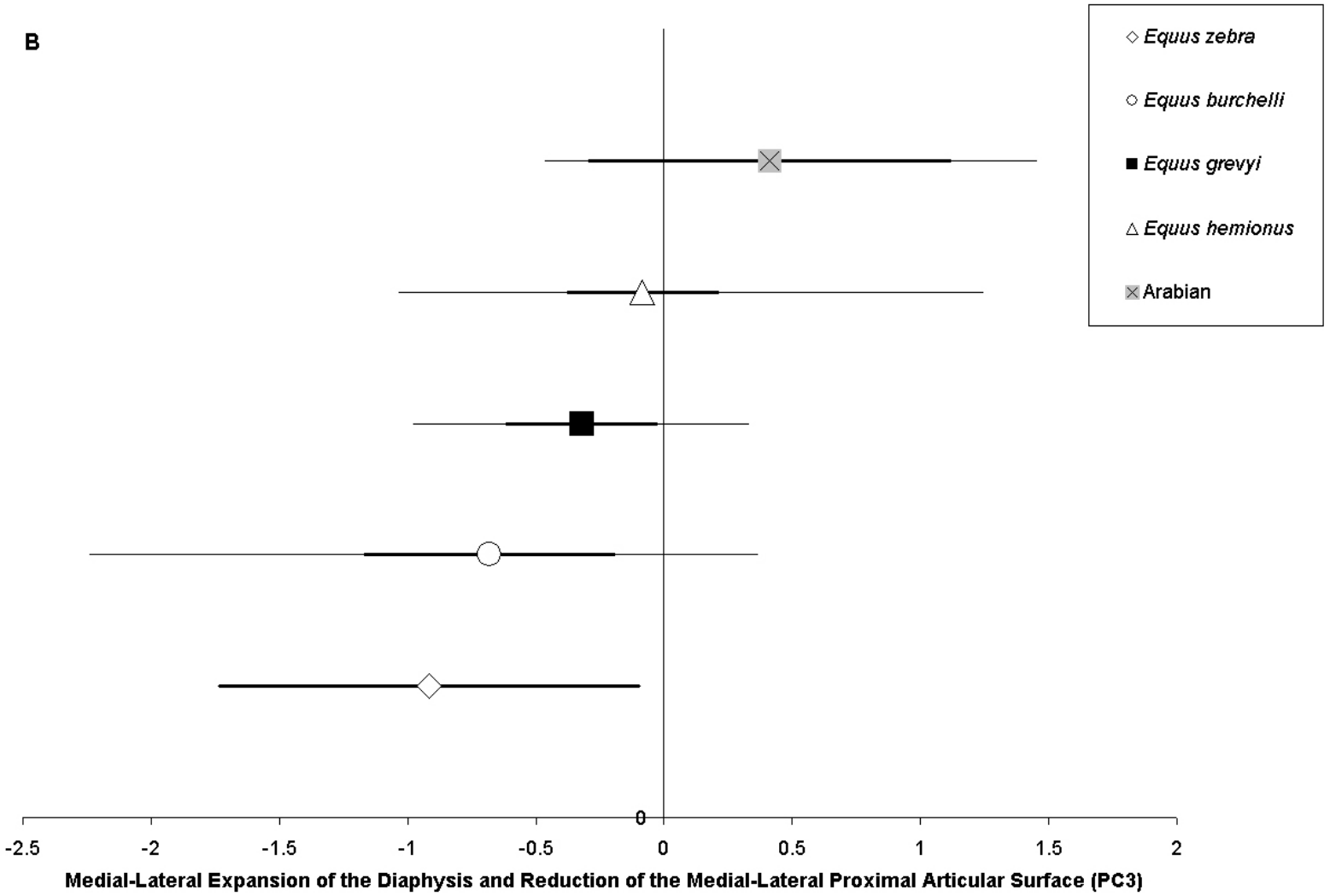


Figure 5.4: Summary plot of PC3 for extant equids. A, MT III's; B, MC III's. Mean principal component scores are shown with 95% confidence intervals denoted by thick lines and ranges shown as thin lines.

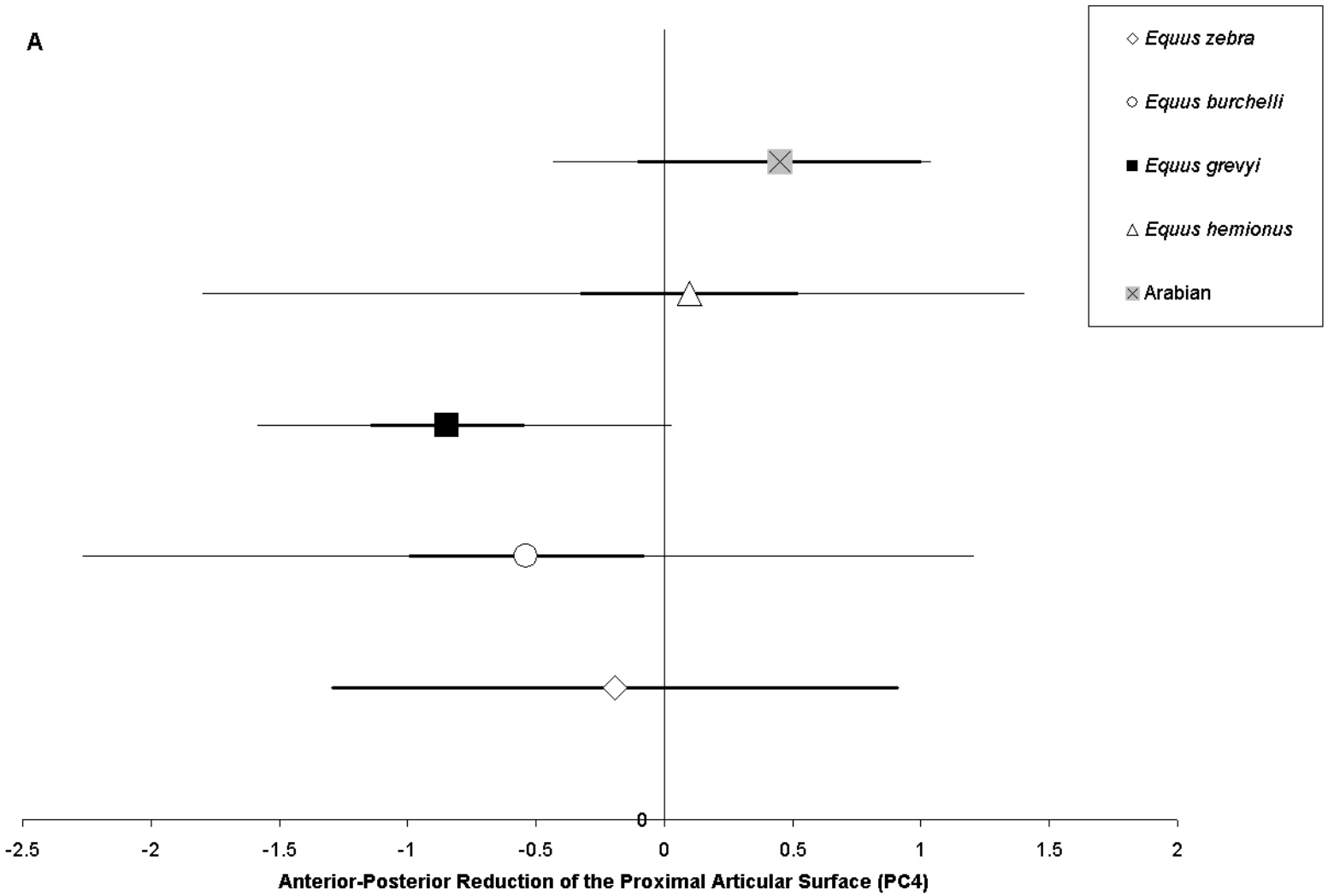


Figure 5.5: Summary plot of PC4 for extant equids. A, MT III's; B, MC III's. Mean principal component scores are shown with 95% confidence intervals denoted by thick lines and ranges shown as thin lines.

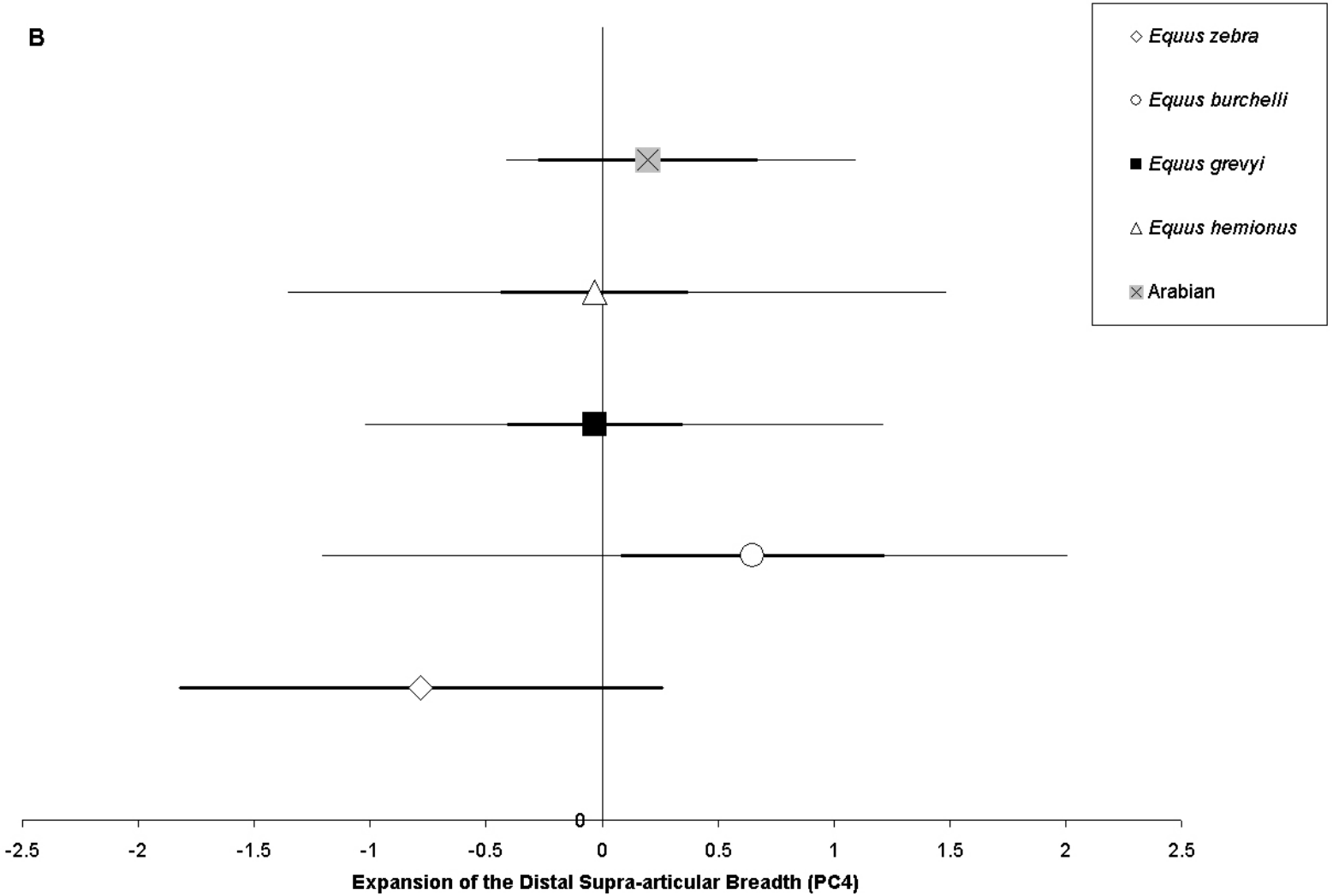


Figure 5.5: Summary plot of PC4 for extant equids. A, MT III's; B, MC III's. Mean principal component scores are shown with 95% confidence intervals denoted by thick lines and ranges shown as thin lines.

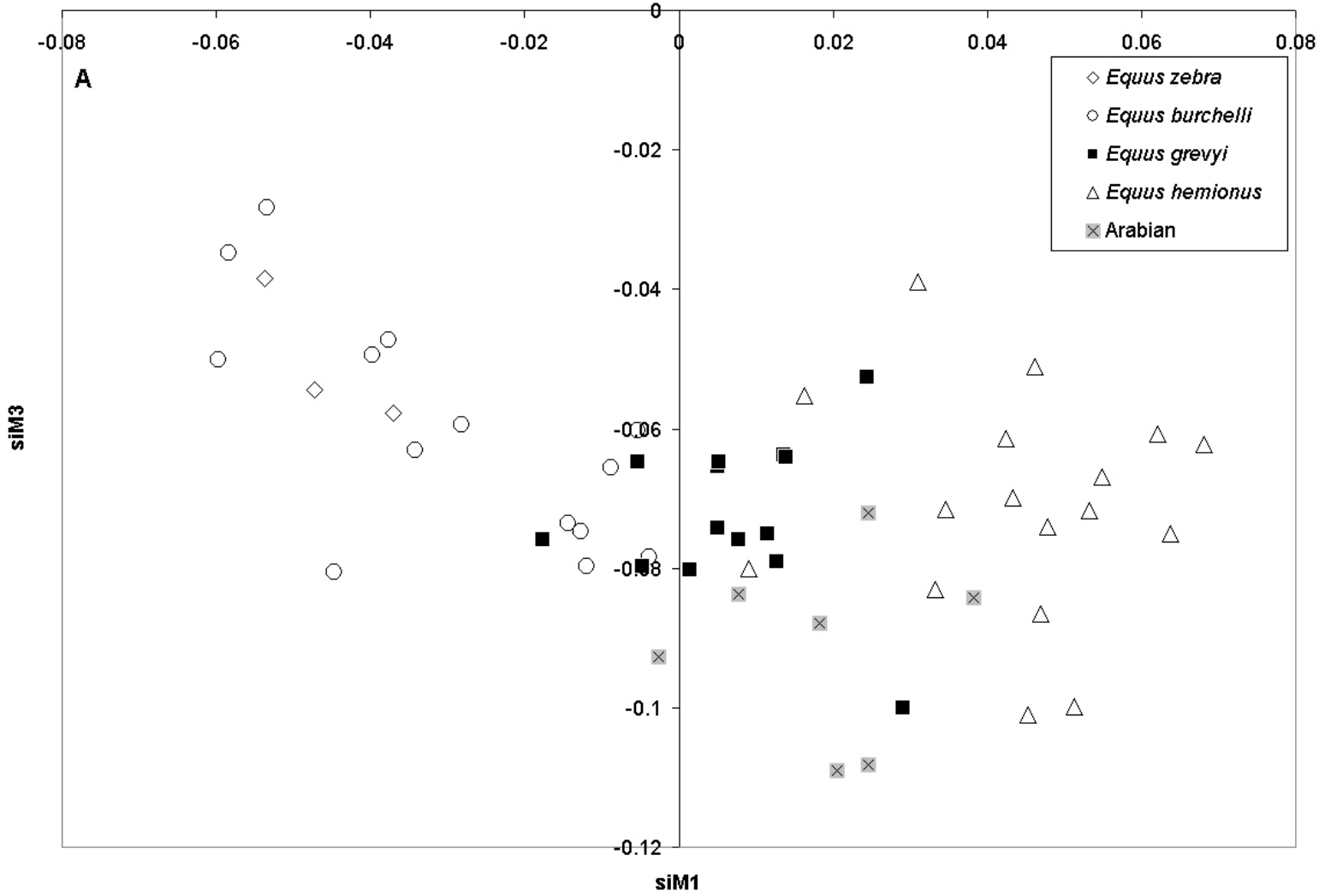


Figure 5.6: Plot of siM3 and siM1 for extant equids. A, MT III's; B, MC III's.

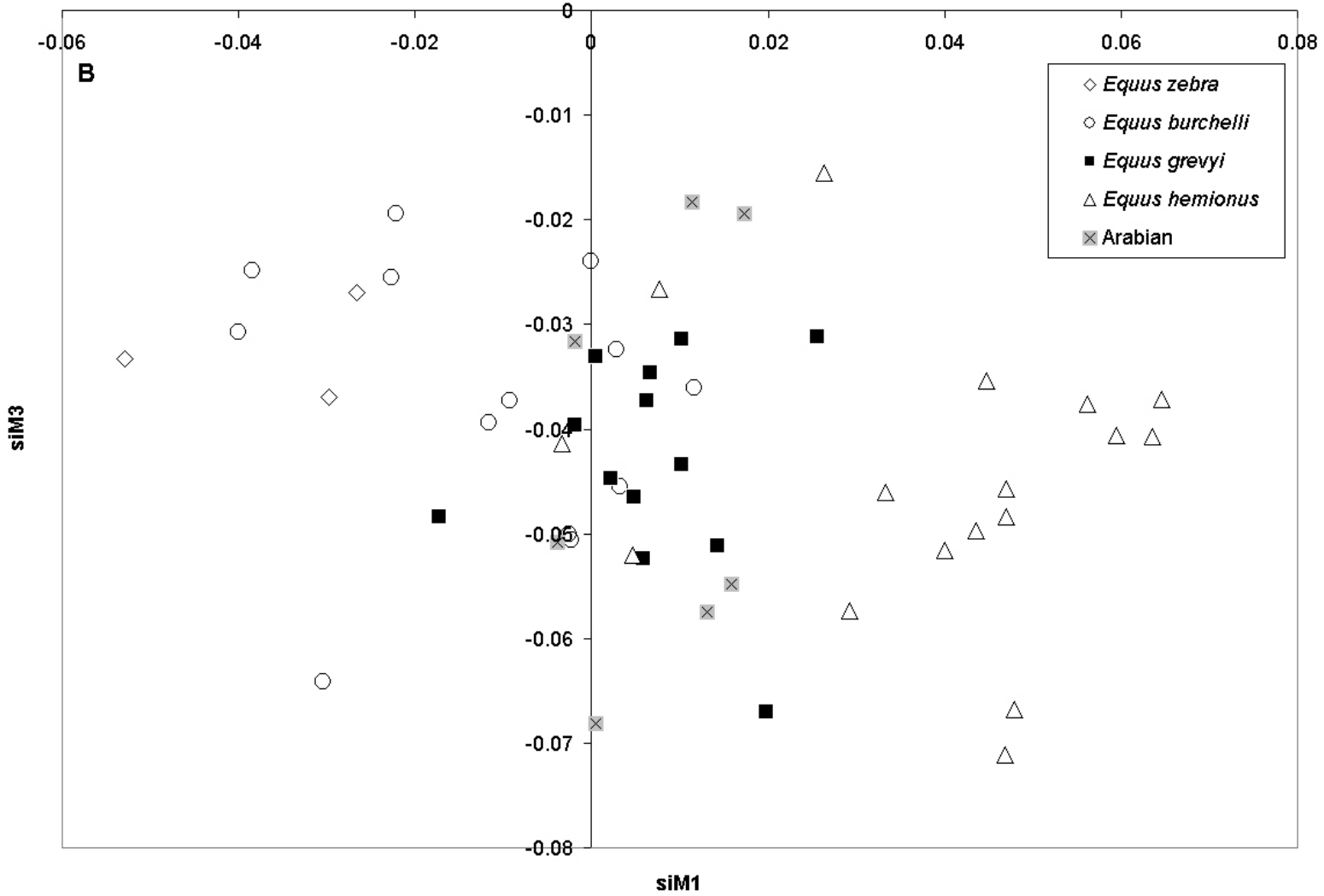


Figure 5.6: Plot of siM3 and siM1 for extant equids. A, MT III's; B, MC III's.

Chapter 6: Fossil Hipparionini

RESULTS

Size independent variable computation

For MT III's, the logged ratios of M1, M3, M4, M10, M11, M13, and M14 over MGSV were correlated with $\log_{10}$(MGSV) ($p < 0.0001$, see tab. 6.1) and residuals were computed for these ratios. These residuals were adopted as size independent shape variables and are referred to as siM1, siM3, siM4, siM10, siM11, and siM14 respectively. The logged ratios for M5, M6, and M12 over MGSV were not significantly correlated with MGSV (tab. 6.1) and these ratios were retained for the remainder of the MT III analysis. They are referred to as siM5, siM6, and siM12.

In the case of MC III's, the logged ratios of all measurements over MGSV except M6 were significantly correlated with $\log_{10}$(MGSV) ($p <0.01$, see tab. 6.1). Thus, residuals were used for siM1, siM3, siM4, siM5, siM10, siM11, siM12, siM13, and siM14 and $\log_{10}$(M6/MGSV) was used for siM6.

Principal components analysis

While PCA will yield principal components equal to the number of variables in the analysis, each additional component explains a smaller proportion of the sample variance and is likely of diminished importance. Accordingly, Scott and Maga (in press) limited discussion to components that explained at least 10% of the sample variance. This rule was applied here.

Metatarsal III

PCA of hipparionine MT III's resulted in four principal components that each accounted for greater than 10% of the total variance. Cumulatively, these four

components explained 76.4% of the variance (tab. 6.2). Of these four components, principal component one (PC1) explained 30.14% of the variance and summarized variability mainly in siM1 and siM3 (tab. 6.3). Increased scores on PC1 corresponded to increased length relative to size as indicated by a positive eigenvector of 0.601 with siM1 and to a decreased medial-lateral dimension of the diaphysis as indicated by a negative eigenvector of -0.537. The next highest eigenvector for PC1 was with siM6 (0.333). These results regarding PC1 are very similar to those of Scott and Maga (in press).

PC2 appears most similar to PC4 in the analysis of Scott and Maga (in press) and expresses the relative expansion of distal dimensions (particularly the crista sagittalis compared to the proximal anterior-posterior dimension). PC2 explained 20.17% of the variance. PC2 appears highest when values of siM6, the anterior-posterior proximal variable, are small and values of siM12, the anterior-posterior variable for the crista sagittalis, are large (tab. 6.3).

PC3 and PC4 appear to describe the morphological axes of general diaphyseal robusticity and expansion of medial-lateral articular dimensions. In this respect, PC3 in this study is like PC2 of Scott and Maga (in press) and PC4 in this study is like PC3 of Scott and Maga (in press). PC3 explained 14.84 % of the total variance and appears to describe overall diaphyseal robusticity. The two highest eigenvectors for PC3 are positive and are with siM3 (0.455) and siM4 (0.594). All other non-length variables have negative eigenvectors with PC2 (tab. 6.3).

PC4 explained 11.24% of the variance and had positive eigenvectors with the medial-lateral dimensions siM5 (0.505), siM10 (0.378), and siM11 (0.329). Thus, PC3 appears to be greatest when the medial-lateral dimensions of the epiphyses are relatively large and in particular when the distal and proximal medial-lateral articular dimensions are great.

Metacarpal III

Principal components analysis (PCA) of the expanded sample of 217 hipparionine MC III's yielded results similar to those obtained by Scott and Maga (in press) with a smaller sample of 126 MC III's. As was the case with Scott and Maga (in press), three principal components were obtained that each explained more than 10% of the sample variance. The eigenvalues and eigenvectors for the MC III PCA are detailed in tables 6.2 and 6.3. PC1 in the MC III analysis explained 35.6% of the variance. PC1 appears to describe relative elongation and slenderness. PC1 had a positive eigenvector of 0.600 with siM1 and a positive eigenvector of 0.443 with siM4. PC1 had a negative eigenvector of -0.491 with the medial-lateral variable siM3.

PC2 explained 18.5% of the variance in the MC III sample and had strong positive eigenvectors with both siM3 (0.450) and siM4 (0.606) as was the case in Scott and Maga (in press). However, PC2 had the strongest eigenvector with siM6 (-0.817). Thus, PC2 appears to express two morphological trends: diaphyseal robusticity and proximal anterior posterior reduction. PC2 in this study appears to resemble PC2 of Scott and Maga (in press) to a lesser degree than PC1 of this study resembles PC1 of Scott and Maga (in press).

PC3 explained 13.2% of the MC III sample variance. PC3 had the strongest eigenvectors with the anterior posterior variables of the distal articulation, siM12 (0.242), siM13 (0.250), and siM14 (0.356), and with the anterior-posterior diaphyseal variable, siM4 (-0.261). Thus, the morphological trend expressed is one of anterior expansion of distal articular surfaces and anterior-posterior reduction of the diaphysis. This result is similar to that of Scott and Maga (in press) for PC3.

Habitat score computation

One significant canonical correlation each was generated for bovid and antilocaprid metatarsals and metacarpals assigned to either the plains or forest habitat groups ($p<0.0001$) based on the variables rcMLEN and rcMML. The resulting canonical variables maximized the separation between the forest and plains groups on the basis of rcMLEN and rcMML. These canonical variables are hereafter considered as possible habitat scores.

The equations generated by the canonical analysis for the computation of habitat scores (HS) are as follows:

Metatarsal HS = (7.596 x rcMLEN) + (-30.063 x rcMML)

Metacarpal HS = 3.718 x rcMLEN) + (-30.494 x rcMML)

Forest bovids have negative habitat scores while plains habitat bovids have positive habitat scores in the case of both metacarpals and metatarsals. Similarly, intermediate habitat bovids which were not part of the sample used to determine the habitat score coefficients appear to differ in terms of habitat score according to the same trend. Heavy cover habitat bovids had a lower mean habitat score than light cover bovids. Mountain forms had lower mean habitat scores than forest forms. In the case of the metatarsals, these differences were significant ($p <.05$, Kruskal-Wallis test). These differences in habitat score can be seen in figure 6.1 where mean habitat scores are shown for each habitat and by species grouped according to subfamily.

The equations used to calculate habitat score for the bovid/antilocaprid sample were applied to the hipparionine sample. The analogous hipparionine variables siM1 and siM3 were substituted for rcMLEN and rcMML. Thus, the habitat score for a specimen is a linear combination of variables summarizing metapodial length and metapodial diaphysis breadth relative to the scaling trend for the that specimen's taxonomic group.

Large habitat scores for hipparionine specimens correspond to metapodials that are slender and elongate compared to other hipparionine specimens while large habitat scores for bovid specimens correspond to metapodials that are slender and elongate compared to other bovid specimens.

For MT III's, the Höwenegg standard, previously interpreted as a forest dwelling hipparionine, had a mean habitat score of -0.74 (N = 20) while the La Roma standard had a mean habitat score of 0.89 (N = 16) (tab. 6.4). *Cremohipparion mediterraneum* from Pikermi has also been used as a comparative standard in studies of hipparionine metapodial morphology (Eisenmann, 1995; Koufos, 2000a). *Cremohipparion mediterraneum* from Pikermi had habitat score of 0.32 (N = 5) (tab. 6.4). In the case of MC III's, *Hippotherium primigenium* VON MEYER 1829 from Höwenegg had a mean habitat score of -0.99 (N = 14), the La Roma hipparion had a mean habitat score of 0.85 (N = 7), and *Cremohipparion mediterraneum* from Pikermi had a mean habitat score of 0.77 (N = 3) (tab. 6.4).

Hipparionine morphometric results by site

The following sections summarize results for hipparionines by site and provide a preliminary estimate of the number of hipparionine species represented by MP III's at each site. Estimation of species number is needed in part to prevent the generation of summary statistics for morphological variables and habitat score that combine data from probably distinct species. Further elaboration of possible species level taxonomy is included in the Discussion.

Bivariate plots were constructed to visually summarize MP III variability in size, relative MP III elongation, and relative MP III slenderness. Since PC1 appears to summarize relative elongation and slenderness for both MT III's and MC III's, it was plotted against the size variable $\log_{10}$(MGSV). M5 had the highest correlation with

MGSV of all the measurements and therefore similar plots were constructed of M1 and M3 versus M5 in some cases. These latter plots made a larger sample available for several sites. The two components of habitat score, the relative length and relative diaphysis breadth variables siM1 and siM3, were also plotted against each other. For comparison, each plot includes 95% confidence ellipses for the Höwenegg and La Roma standards.

Principal component scores are summarized by site and species for PC1-PC4 for MT III's and for PC1-PC3 for MC III's in table 6.5. Habitat scores are summarized by site and species in table 6.4.

Fossil hipparionines from Spain

Los Valles de Fuentidueña

One complete MC III and four complete MT III's were available for study from the site of Los Valles de Fuentidueña (Segovia, Spain) in the Duero Basin. The four MT III's shown in figure 6.2A are within the 95% confidence ellipse for the La Roma standard in terms of relative elongation and slenderness (siM1 and siM3) and contrast with the Höwenegg standard. The single MC III from Los Valles de Fuentidueña sits just outside the La Roma 95% confidence ellipse but is clearly relatively slender and in sharp contrast to the Höwenegg standard (fig. 6.2B). Figure 6.3 distinguishes the complete Los Valles de Fuentidueña MT III's and MC III from the La Roma and Höwenegg standards in terms of the size variable MGSV. These specimens clearly represent a species much smaller than that from La Roma and slightly smaller than *Hippotherium primigenium* from Höwenegg. In terms of relative MP III elongation and slenderness as expressed by PC1, the Los Valles de Fuentidueña hipparion has high scores for PC1 and clearly appears relatively long and slender (fig. 6.3).

Additional less complete MT III's were available from Los Valles de Fuentidueña. A total of eight MT III's from Los Valles de Fuentidueña preserved the M5, M1, and M3 dimensions and are plotted in figures 6.4A and 6.5B. These plots confirm a smaller sized species of hipparion with relatively small M3 dimensions and large M1 dimensions. 95% confidence ellipses of these eight MT III's for M1 versus M5 and M3 versus M5 constrain the Los Valles de Fuentidueña specimens in a tight cluster most consistent with a single species of hipparion.

Among other Spanish hipparionines shown (figs. 6.2-5) those from El Lugarejo appear most comparable to those from Los Valles de Fuentidueña. The single complete MT III from El Lugarejo is within the 95% confidence ellipses for M1 versus M5 and M3 versus M5 of MT III's from Los Valles de Fuentidueña (figs. 6.4 & 6.5). Scores for PC1 are comparable between El Lugarejo and Los Valles de Fuentidueña (tab. 6.5; fig 6.3). In terms of MGSV, it appears that the MP III specimens from El Lugarejo derived from somewhat smaller hipparions than those from Los Valles de Fuentidueña (fig 6.3).

The mean habitat score for the Los Valles de Fuentidueña hipparion was 0.74 based on the four complete MT III's (tab. 6.4). The single complete MC III from Los Valles de Fuentidueña resulted in a habitat score of 0.95 (tab. 6.4).

El Lugarejo

El Lugarejo (Avila, Spain) is a second fossil locality of the Duero Basin and two complete MC III's and one complete MT III were available for study. The specimens from El Lugarejo appear comparable to those from Los Valles de Fuentidueña (fig 6.2) in terms of relative elongation and slenderness. The MC III's from El Lugarejo appear somewhat smaller in size than those from Los Valles de Fuentidueña (fig. 6.3). A third MC III preserved the M5, M1 and M3 measurements and is plotted in figures 6.4B and 6.5B. The three MC III's shown here appear to be smaller than the only preserved MC III

from Los Valles de Fuentidueña. In general, the MP III's from El Lugarejo compare favorably with those from Los Valles de Fuentidueña.

Habitat scores for specimens from El Lugarejo were: 0.62 and 0.27 for the two MC III's and 0.40 for the one MT III (tab. 6.4).

Santiga

Santiga (Sabadell, Spain) is the best sampled of the MN 9 sites of the Vallés-Penedés Basin in terms of complete MP III's. Four complete MT III's and four complete MC III's were available for study here.

In terms of the relative elongation and slenderness dimensions, the Santiga MT III's plot within the Höwenegg 95% confidence ellipse, although they have values for the relative length dimension (siM1) that are towards the low end of the Höwenegg range (fig. 6.2A). The Santiga MC III's have very negative values for siM1 and plot to the left of the Höwenegg 95% confidence ellipse (fig. 6.2B). The Santiga sample is clearly distinguished by relatively short and broad metapodials with the relative shortening of MC III being particularly pronounced.

The short and broad character of the Santiga MP III's is confirmed by negative scores for PC1 (see fig. 6.3; tab. 6.5). The Santiga specimens also appear small in terms of overall size with low values for MGSV (fig. 6.3). The Santiga hipparion appears to have been smaller than *Hippotherium primigenium* from Höwenegg and to have had relatively shorter MP III's.

Collectively, the Santiga specimens plot close together and would appear to constitute a single species of hipparion. The MC III and MT III specimens are concordant in their morphology and it would appear unlikely that the MC III's and MT III's sampled different species. The MT III IPS-1555 is somewhat longer than the other MT III's from

Santiga that preserve the M1 dimension and is the only possible outlier in the Santiga sample.

The Santiga sample of MP III's also appears to suggest a species of hipparion distinct from other Spanish hipparions. Other Spanish hipparions appear to be either more elongate than the Santiga specimens or smaller in size (figs. 6.2 & 6.3). Values of siM1 for the Santiga MC III's do not overlap the range of siM1 values for all other Spanish hipparions (fig. 6.2).

The Santiga hipparions yielded extremely negative habitat scores. The Mean habitat score for MC III's was -1.01 and for MT III's was -1.06 (tab. 6.4).

Can Llobateres

Four complete MC III specimens from Can Llobateres appear distinguishable from the Höwenegg standard mainly in terms of relative slenderness. These specimens mostly plot below the 95% confidence ellipse for the Höwenegg standard indicating an apparently somewhat more slender diaphysis as indicated by lower values for siM3 (fig. 6.2B). However, the Can Llobateres MC III's are more comparable to those from Höwenegg in terms of PC1 and MGSV and appear to occupy the lower end of the size spectrum and upper end of the relative elongation and slenderness spectrum for the Höwenegg sample (fig. 6.3B). The MC III's from Can Llobateres are on the whole suggestive of a hipparion that is smaller in size with relatively more slender MC III's than *Hippotherium primigenium* from Höwenegg.

Five added MC III's from Can Llobateres preserved the M5, M1 and M3 dimensions and are plotted with the better preserved specimens in figures 6.4B and 6.5B. A 95% confidence ellipse for the Can Llobateres sample is large and suggests a more variable sample than that from Höwenegg. The plot of M3 versus M5 includes only one MC III from Can Llobateres that plots within the Höwenegg 95% confidence ellipse. The

remaining specimens tend to plot below and to the left of the Höwenegg 95% confidence ellipse. Thus, some specimens suggest a hipparion that is on average smaller than *Hippotherium primigenium* from Höwenegg while others suggest a form with more slender MC III's.

Three complete MT III's are plotted in figure 6.2A and just fit within the Höwenegg 95% confidence ellipse. These specimens however plot towards the low end for the Höwenegg standard in terms of MGSV (fig. 6.3A). The plots of M1 versus M5 and M3 versus M5 include one less well preserved MT III (figs. 6.4A & 6.5A) and this specimen appears larger with a greater value for M5.

It appears that more than one hipparion species is possible for Can Llobateres. If this is the case, then one species from Can Llobateres would appear to have more slender MC III's than *Hippotherium primigenium* from Höwenegg but be similar in size. This species could be represented by the three MC III's that plot below the Höwenegg 95% confidence ellipse and are distinguished by lower values for siM3.

A second species that is smaller in size but similar in shape to *Hippotherium primigenium* from Höwenegg could be represented by the MC III that plots within the Höwenegg 95% confidence ellipse in fig. 6.2B. Other less complete MC III's could also be attributed to this smaller species (figs. 6.4B & 6.5B). The small form from Can Llobateres would then appear similar in size to the hipparion form Santiga but with values of siM1 and siM3 that are comparable to those of *Hippotherium primigenium* from Höwenegg.

The two apparent Can Llobateres species are shown in fig. 6.6 clustered around their respective scaling trends (best fit least squares regression lines) for M3 versus M5. One has smaller measurements for M5 (i.e.; the small species) while the other has smaller measurements for M3 compared to M5 (i.e., the species with more slender MP III's.

Applying the partitioning suggested based on MC III's would lead to putting the three well-preserved MT III's shown in figures 6.2A and 6.3A in the smaller species. One larger less well-preserved specimen would be most parsimoniously assigned to the larger species with more slender MC III's.

Based on this partitioning of the Can Llobateres sample, the smaller species would have a mean habitat score of -0.43 (N = 3) based on MT III's. The well-preserved MC III attributed to this smaller species results in a habitat score of -0.55. The mean habitat score based on MC III's for the larger species from Can Llobateres would be 0.10 (N = 3).

Polinya

An MC III from Polinya plots with the more slender and larger specimens from Can Llobateres but also appears more like the smaller specimens from Can Llobateres in terms of size (figs. 6.4B & 6.5B). The habitat score for this specimen is -0.14.

Can Ponsic

M5, M1 and M3 are available for a single MT III from the Vallés-Penedés Basin MN 9 locality of Can Ponsic and this specimen compares favorably with the smaller MT III's from Can Llobateres (figs. 6.4A & 6.5A).

La Tarumba and Villadecavalls vicinity

One well-preserved complete MC III from La Tarumba (Villadecavalls, Spain) plots with the MC III's from Can Llobateres attributed to a larger species with somewhat more slender MC III's than *Hippotherium primigenium* from Höwenegg (figs. 6.2B & 6.3B). A second MC III is less well-preserved but may fit with a smaller species at Can Llobateres. The habitat score generated for the better preserved La Tarumba MC III was -0.10 (fig. 6.6).

One MT III appears to be from the Villadecavalls vicinity although the exact provenience is uncertain (Can Trullas, Can Porull, or La Tarumba). This specimen was not complete enough to generate a habitat score but it appears comparable in size with *Hippotherium primigenium* from Höwenegg (figs. 6.4A & 6.5A) and somewhat more elongate (fig. 6.4A).

Piera

Plots of M1 versus M5 and of M3 versus M5 for MC III's from Piera resulted in 95% confidence ellipses that constrain the Piera specimens tightly (figs. 6.4B & 6.5B). This result suggests only a single species at Piera (or at the very least that any additional species would be quite rare).

Morphologically, the Piera hipparion appears smaller than *Hippotherium primigenium* from Höwenegg and similar in terms of relative slenderness and elongation to the smaller MC III's from Can Llobateres and Höwenegg standard (figs. 6.2B-5B). Some of the Piera MC III's have lower values for siM3 indicating a possible slight tendency towards more slender MC III's and the possibility of being intermediate between the two Can Llobateres forms in terms of MC III relative slenderness.

MT III's from Piera are less well-sampled than MC III's and mainly confirm a favorable comparison with the smaller MT III's from Can Llobateres.

The habitat scores for the Piera hipparion were -0.27 based on MC III's (N = 6) and 0.14 based on MT III's (N = 2).

Nombrevilla

No specimens from Nombrevilla were complete enough to generate habitat scores, however, two MC III's could be plotted in figures 6.4B & 6.5B. These specimens would appear similar in size to *Hippotherium primigenium* from Höwenegg and the

larger Can Llobateres form. Values for M3 and M1 appear to be at the maximal extremes for the Höwenegg sample. The Nombrevilla MC III's are just outside the Höwenegg 95% confidence ellipse for M1 versus M5 due to longer M1 measurements. They are just inside the Höwenegg 95% confidence ellipse for M3 versus M5 with very great M3 measurements. It is difficult to extrapolate where the Nombrevilla MC III's would plot in figures 6.2B and 6.3B if all measurements were known for them. However, the M1, M3, and M5 measurements are consistent with a hipparion slightly larger and similar to *Hippotherium primigenium* from Höwenegg.

La Roma 2

The La Roma 2 MP III's appear clearly distinct in terms of size and shape and also fit within well-constrained 95% confidence ellipses (figs. 6.2 & 6.3). Figure 6.2A plots the siM1 and siM3, the major determinants of PC1, for La Roma 2 MT III's (N = 16). The Höwenegg and La Roma 2 standards are plotted as 95% confidence ellipses and have a very narrow range of overlap. The Höwenegg specimens generally have negative scores for siM1 and positive scores siM3. The La Roma 2 specimens contrast with the Höwenegg sample on both of these axes and generally have positive values for siM1 and negative values for siM3. Thus, the La Roma 2 MT III's clearly describe a hipparion species large in size with elongate and slender MT III's.

The same morphological trends seen in the La Roma 2 MT III's are evident for the La Roma 2 MC III's. The 95% confidence ellipses for Höwenegg and La Roma do not overlap and plot in contrasting quadrants in figure 6.2B Höwenegg tends to have negative values for siM1 and positive values for siM3 while La Roma has positive values for siM1 and negative values for siM3. Similarly, figure 6.3B reflects the large size and relative elongation and slenderness of the La Roma 2 MC III's.

The habitat scores for the La Roma 2 hipparion were 0.85 for MC III's and 0.89 for MT III's (tab. 6.4).

Concud

The site of Concud is found in the Teruel area of the Calatayud-Teruel Basin like La Roma 2 but has a younger mammal correlation of MN 12 (Alcalá, 1994; Morales et al., 1999; NOW, n.d.). The Concud sample studied here is housed in the MNCN and includes seven MC III's and six MT III's that were complete enough for PCA and generation of habitat scores. A few added specimens preserved M5 and M1 or M5 and M3 and could be plotted in figures 6.4 & 6.5. In total: Nine MC III's preserved M5 and M3; eight MC III's preserved M5 and M1; seven MT III's preserved M5 and M3; and eight MT III's preserved M5 and M1.

Confidence ellipses for the Concud MT III's (figs. 6.4A & 6.5A) suggest a range of MT III variability consistent with that seen from Los Valles de Fuentidueña, Höwenegg, and La Roma 2. No argument for multiple species from Concud would appear tenable on the basis of MT III's. In contrast, the Concud MC III's appear more variable in terms of MC III's. The range of variation in siM3 appears extreme for the Concud MC III's with some specimens appearing relatively broad like the Höwenegg standard and some appearing relatively slender like the La Roma 2 standard (fig. 6.2B). The broad range of siM3 for the Concud MC III's translates into two distinct groupings of specimens in terms of PC1 and a large 95% confidence ellipse for PC1 versus MGSV (fig. 6.3B). Similar large confidence ellipses can be seen in figures 6.4B & 6.5B apparently driven by variability in size and relative slenderness.

Splitting the Concud sample is difficult to justify on the basis of variability seen mainly in terms of relative slenderness of the MC III only. Without greater variability in size or similar morphological bimodality observed for MT III's, partitioning the Concud

sample into two species can be viewed as problematic. However, it is worth observing the clear bimodality in shape observed for the Concud MC III's in terms of relative slenderness. Consequently, a slender morph and broad morph are recognized for the Concud MC III's.

The mean habitat score for the Concud MT III's was -0.59 (N = 6). The mean habitat score for the total sample of Concud MC III's was -0.29 (N = 7). When the Concud MC III habitat scores are summarized after the sample is partitioned into a slender and a broad morph, the mean habitat scores are 0.28 (N = 4) and -1.05 (N = 3) respectively.

La Gloria 4

The MT III identified as *Hipparion* cf. *elegans* GROMOVA 1952 by Eisenmann and Mein (1996) from the MN 14 locality La Gloria 4 in the Teruel area of the Calatayud-Teruel Basin resulted in a habitat score of 1.27. This specimen is clearly relatively long in the extreme and, in contrast to a similarly elongate specimen from Layna, relatively slender (fig. 6.2A). This MT III also belongs to a hipparion smaller than *Hippotherium primigenium* from Höwenegg (fig. 6.3A).

El Firal

El Firal (Seu d'Urgell, Spain) in the Seu d'Urgell Basin is known for specimens of the hominoid *Dryopithecus fontani* (Smith-Woodward, 1914; Simons & Pilbeam, 1965; Begun, 1992a; Begun, 1992b; Andrews et al., 1996) and therefore is briefly noted here. No hipparionine MP III's from El Firal preserved the M3 or M1 dimensions so little description is possible. Three MC III preserved the M5 dimension and the range of M5 measurements for these specimens was 36.49 – 38.95 mm which overlapped the ranges for both the larger and smaller Can Llobateres MC III's and the lower part of the

Höwenegg range. A hipparionine that was on average smaller than *Hippotherium primigenium* from Höwenegg appears most plausible.

Ballestar

One MT III (BA019) was available for study from the MN 9, *Cricetulodon* Zone locality of Ballestar (Ballestar, Spain) in the Seu d'Urgell Basin (Agusti, 1982). This specimen compares most closely with the smaller MT III's from Can Llobateres: smaller in size than *Hippotherium primigenium* from Höwenegg but similar in shape (figs. 6.2B-6.5B). However, BA019 also plots inside the Höwenegg 95% confidence ellipses in figures 6.2B-5B. Without a larger sample from Ballestar it is not possible to distinguish the Ballestar MT III from either *Hippotherium primigenium* from Höwenegg or the smaller specimens from Can Llobateres. BA019 is in fact a very plausible intermediate between *Hippotherium primigenium* from Höwenegg and the smaller Can Llobateres specimens. The habitat score for BA019 was 0.10.

One MC III (BA015) from Ballestar preserves the M5, M1, and M3 measurements. Based on M5 and M1 (fig. 6.4B) BA015 can not be distinguished from *Hippotherium primigenium* from Höwenegg. However, it is also impossible to rule out conspecific status with larger MC III's from Can Llobateres.

Venta del Moro

MP III's (one MT III and two MC III's) from Venta del Moro (MN 13) describe a hipparion quite small in size with relatively elongate and slender MP III's (figs. 6.2-5). The habitat scores for Venta del Moro MP III's were 0.75 and 0.80 for the two MC III's and 0.97 for the MT III.

Layna

One MT III (ISP 2104) from Layna (Soria, Spain) in the Tajo Basin correlated to MN 14 and identified as *Hipparion fissurae* CRUSAFONT & SONDAAR 1971 (Eisenmann & Mein, 1996; NOW, n.d.) was included in this study. ISP 2104 resulted in a habitat score of -0.36. This score is low given very high values of siM1 for ISP 2104. The high value for siM1 is accompanied by a high value for siM3 in the case of ISP 2104 (fig. 6.4A). The low habitat score appears to reflect the influence of siM3.

Fossil hipparionines from Greece

Pikermi

Since Hensel (1862), two common MP III morphologies have been recognized at Pikermi: a form with elongate, slender metapodials and a form with short, robust metapodials. These results are replicated here with material from Pikermi in the MNHN collections. A group of more elongate and slender MP III's from Pikermi is smaller in size and has higher scores for PC1 than (fig. 6.7). The contrast between these two groups of MP III's can also be seen in figure 6.8 where siM3 and siM1 are plotted. One group is distinguished mainly by higher values for siM1 (relative elongation) in contrast to the other MP III's from Pikermi (fig. 6.8). In the case of MC III's, there also appears to be a strong contrast in terms of siM3 (relative slenderness, see fig. 6.8B) although the sample of MC III's studied is smaller.

The smaller more elongate MP III's from Pikermi resulted in mean habitat scores of 0.77 and 0.32 based on MC III's and MT III's respectively. The larger, relatively shorter MP III's from Pikermi had negative habitat scores with mean values of -0.53 based on MC III's and -0.57 based on MT III's.

Samos

The situation at Samos with respect to hipparionines is complex. Samos includes several fossiliferous horizons which span MN 11 to the top of MN 12 or base of MN 13 (Kostopoulos et al., 2003). Provenience of specimens is occasionally unknown and many collections include specimens from Samos collected at different times under various conditions. Various workers have recognized that many species are represented at Samos and that multiple species often derive from a single locality (Sondaar, 1971; Forsten, 1980; Bernor et al., 1996b; Bernor et al., 1996c). The results for MP III specimens from Samos discussed here confirm the great variability among hipparionines from Samos and are presented here first by size and second by apparent morphological group. Based on size and morphology, specimens are assigned to "Morphs" as a provisional classification. Each "Morph" is considered as probably sampling conspecifics and when possible assumptions are made to minimize the number of "Morphs" described. The procedure followed here is much like that followed by Bernor et al. (Bernor et al., 2003b). This provisional classification is shown in table 6.6.

MC III's from Samos appear to fit into three size groupings while MT III's may constitute four size groupings. Among MC III's and MT III's, there are specimens that plot to the left of the Höwenegg 95% confidence ellipse for PC1 plotted versus MGSV (fig. 6.9). In the case of MC III's, these specimens do not appear to be further divisible on the basis of size alone. However, the ten smaller MT III's from Samos appear to include four that are much smaller than the Höwenegg standard (fig. 6.9A). These four specimens also appear to be smaller than those of *Cremohipparion mediterraneum* from Pikermi and comparable in size to *Cremohipparion macedonicum* from Ravin de la Pluie (fig. 6.9A). The MC III's from Samos that are to the left of the Höwenegg 95% confidence ellipse appear comparable to specimens of *Cremohipparion mediterraneum* from Pikermi (fig.

6.9B). Thus, it is possible that the four smallest MT III's from Samos represent a form of hipparion not represented by MC III's. In terms of size, the remaining MP III's from Samos appear to fit within one of two additional groupings: 1) specimens within the size range for Höwenegg or 2) specimens that are above the size range for Höwenegg (fig. 6.9).

In terms of morphology, most of the MC III's from Samos appear to form a morphologically uniform cluster of relatively elongate and slender specimens (Samos Small Elongate Morph in fig. 6.10B). These five MC III specimens have positive scores for PC1 (fig. 6.9B) and plot above the right side of the La Roma 2 95% confidence ellipse for siM3 versus siM1 (fig. 6.10B). Thus, they would appear relatively long compared to the La Roma 2 standard and not quite as relatively slender but clearly relatively more slender than the Höwenegg standard. Compared to *Cremohipparion mediterraneum* from Pikermi the Samos Small Elongate Morph specimens are relatively longer but also relatively broader which results in what are on the whole very similar scores for PC1 (figs. 6.9B & 6.10B). One additional less well-preserved specimen is added to the Samos Small Elongate Morph in figures 6.11 & 6.12 plotting M1 and M3 versus M5. Based on MC III's, the mean habitat score for the Samos Small Elongate Morph was 0.11.

Two additional smaller MC III's from Samos had quite negative scores for PC1. These two specimen were however quite different in size from each other (fig. 6.9B). The smaller of these two MC III's (AMNH FM140292) is from Quarry 6 which is likely older than the other Samos deposits (Kostopoulos et al., 2003). AMNH FM140292 plots within the Höwenegg 95% confidence ellipse for siM3 versus siM1 and is distinctly shorter compared to Samos Small Elongate Morph (figs. 6.9B & 6.10B). This specimen is designated here as representative of the Samos Small Shortened Morph and had a habitat

score of -0.90. The other smaller MC III from Samos with a negative score for PC1 is larger (fig. 6.9B) and seems to compare favorably with specimens designated as "*Hippotherium" brachypus* HENSEL 1862 from Pikermi and is designated as the only representative of the Samos Midsized Shortened Morph. The habitat score for this specimen was -0.36.

Five additional smaller MC III's from Quarry 5 at Samos have been discussed previously (Bernor & Scott, 2003) and these specimens could be plotted in figures 6.11 & 6.12. They look to be smaller than the other Samos MC III's. Two of these specimens compare very nearly with AMNH FM140292 from Quarry 6 and are considered additional examples of the Samos Small Shortened Morph. The three smallest MC III's may group with the very smallest MT III's from Samos which also come from Quarry 5.

As already noted, the four smallest MT III's from Samos appear to be smaller than *Cremohipparion mediterraneum* from Pikermi and about the size of *Cremohipparion macedonicum* from Ravin de la Pluie and likely represent a different species than the Samos Small Elongate Morph MC III's. These four specimens are all relatively elongate but vary in terms of relative slenderness (fig. 6.10A). These MT III's are assigned to the Samos Dwarf Elongate Morph and resulted in a mean habitat score of 0.15. The three smallest MC III's also from Quarry 5 were also assigned to the Samos Dwarf Elongate Morph and are plotted in figures 6.11 & 6.12.

The six other smaller MT III's from Samos also had elevated scores for PC1 and appear to be comparable is size to *Cremohipparion mediterraneum* from Pikermi (fig. 6.9A). Based on size, these specimens would be candidates for inclusion in the Samos Small Elongate Morph. However, these six specimens appear variable in terms of relative slenderness and relative elongation (fig. 6.10A).

Two MT III's from Quarry 4 plot below the La Roma 2 95% confidence ellipse in figure 6.10A and are both elongate and extremely slender. These two specimens have very high scores for PC1. In contrast, another MT III that is similar in size but from Quarry 5 is similarly elongate but is relatively broad and plots above the La Roma 2 95% confidence ellipse (fig. 6.10A). Considering the magnitude in the contrast in MT III morphology between MT III's and their differing provenience and age, it would appear reasonable to consider them as representing different species. The better preserved MC III's identified as representing the Samos Small Elongate Morph included two from Quarry 5, one from Quarry 1, and two others of uncertain provenience. If the MT III's and MC III's from Quarry 5 of similar size and morphology are considered as probably conspecific then the broader, elongate MT III from Quarry 5 (AMNH 22914) can be assigned to the Samos Small Elongate Morph. The two MT III's from Quarry 4 that plot below the La Roma 2 95% confidence ellipse for siM3 versus siM1 (fig. 6.10A) are assigned to a separate Samos Small Slender Morph. A small MT III from Quarry 1 and another small MT III of uncertain provenience that plot within the La Roma 2 95% confidence ellipse for siM3 versus siM1 (fig. 6.10A) were also grouped in the Samos Slender Morph with the two Quarry 4 specimens. A sixth MT III comparable to *Cremohipparion mediterraneum* from Pikermi in size was more like AMNH 22914 from Quarry 5 (i.e., elongate but broad, see fig. 6.10A) and accordingly was grouped with AMNH 22914 in the Samos Small Elongate Morph. Based on MT III's the Samos Small Elongate Morph yielded a mean habitat score of -0.11 and the Samos Small Slender Morph yielded a mean habitat score of 1.62.

Figure 6.9B includes four MC III's similar in size to *Hippotherium primigenium* from Höwenegg but with on average an elevated score for PC1. These same specimens plotted in figure 6.10B would in general appear to be relatively more elongate than

Hippotherium primigenium from Höwenegg but less so than the Samos Small Elongate Morph. Thus, these four MC III's are assigned to the Samos Midsize Elongate Morph. The mean habitat score for the Samos Midsize Elongate Morph is -0.36 based on MC III's.

Three other MC III's appear to be larger in size than *Hippotherium primigenium* from Höwenegg and less elongate compared to the Samos Midsize Elongate Morph (figs. 6.9B & 6.10B). These specimens are assigned to the Samos Large Morph and result in a mean habitat score of -0.15.

Three MT III's are also larger in size than *Hippotherium primigenium* from Höwenegg (fig. 6.9A) and can reasonably be assigned to the Samos Large Morph. Like their MC III counterparts, these specimens do not appear either relatively elongate or relatively slender (fig. 6.10A). Six other MT III's appear comparable to *Hippotherium primigenium* from Höwenegg in size (fig. 6.9A). Four of these MT III's have similar scores for PC1, are relatively elongate, and plot to the right of the Höwenegg 95% confidence ellipse in figure 6.10A. These specimens are best assigned to the Samos Midsized Elongate Morph. Two other MT III's are problematic. These specimens have very low values for PC1 but for different reasons. One is relatively broad and one is relatively short. The relatively broad but elongate specimen is smaller and may be fit in the Samos Midsize Elongate Morph while the relatively short specimen is larger than other members of the Samos Midsize Elongate Morph and is probably best placed in the Samos Large Morph. As composed, the Samos Large Morph results in a mean habitat score of -0.38 based on MT III's and the Samos Midsize Elongate Morph results in a mean habitat score of 0.05 based on MT III's.

Ravin de la Pluie

A few MT III's from the *Ouranopithecus* locality of Ravin de la Pluie in the Axios Valley (Macedonia, Greece) have been reported by Koufos (2000b) and these specimens were analyzed here. These three Ravin de la Pluie MT III's each plot in contrasting quadrants in figures 6.7A & 6.8A.

RPl-38 appears largely comparable to the smallest MT III's from Samos in both figures 6.9A & 6.10A. It is slender and elongate and plots at the right margin of the La Roma 2 95% confidence ellipse in the plot of siM3 versus siM1 (fig. 6.8A & 6.10A). RPl-38 has a slightly lower value for siM3 (greater slenderness) than the smallest Samos MT III's (fig. 6.10A). RPl-38 resulted in a habitat score of 1.32.

RPl-61 contrasts strongly with RPl-38 in terms of morphology. In particular, RPl-61 is relatively shorter and plots in the Höwenegg 95% confidence ellipse in the plot of siM3 versus siM1 (fig. 6.8A). In terms of overall size, RPl-61 is smaller that the MT III's from Höwenegg but larger than RPl-38 (fig. 6.7A). The habitat score for RPl-61 was 0.09.

RPl-39 is the largest of the three MT III's and is comparable to the Höwenegg MT III's in terms of size and its score for PC1. It plots inside the Höwenegg 95% confidence ellipse in figure 6.7A. RPl-39 plots within the Höwenegg 95% confidence ellipse in terms of siM3 and siM1 but does have a positive value for siM1 (relative elongation) (fig. 6.8A). The habitat score for RPl-39 was -0.31.

Saloniki

Four MT III's and two MC III's are shown in figures 6.7-10. The MT III's from Saloniki span the size range from the larger of the Samos MT III's assigned to the Samos Dwarf Elongate Morph and *Cremohipparion macedonicum* from Ravin de la Pluie through the size range of smaller and elongate MT III's from Pikermi (figs. 6.7A &

6.9A). These MT III's have positive scores for PC1 and are similar in elongation (siM1) to the Samos Dwarf Elongate Morph and the smaller elongate MT III's from Pikermi (figs. 6.8A & 6.10A). However, these specimens also appear on average more slender and have lower values for siM1 most comparable to the Samos Small Slender Morph (fig. 6.10A). The resulting mean habitat score is an elevated 1.15.

The two MC III's from Saloniki appear to present a slightly contrasting trend in terms of morphology and size. One specimen is comparable in size to smaller MC III's from Pikermi while the other is comparable in size to the larger MC III's from Pikermi (fig. 6.7A). Both specimens have elevated scores for PC1 (fig. 6.7A) and are elongate like the smaller specimens from Pikermi (fig. 6.8A). However, while the MT III's from Saloniki are slender compared to the small Pikermi MT III's, the Saloniki MC III's are broad compared to the smaller MC III's from Pikermi (fig. 6.8A). The habitat scores for these MC III's (-0.54 and 0.96) were lower than the mean habitat score for the Saloniki MT III's (1.15). It would appear that at least one of the MC III's from Saloniki could possibly represent a second larger hipparion species than the other MP III's from Saloniki.

Maramena

Two MT III's from Maramena are plotted in figures 6.7A & 6.8A and appear comparable smallest MT III from Ravin de la Pluie (= *Cremohipparion macedonicum*) as well as the smallest MT III's from Samos. They appear to represent a very small hipparion with elongate MT III's. The mean habitat score based on these two specimens was 0.35.

Fossil hipparionines of Central Europe

Höwenegg

The Höwenegg hipparion has been treated extensively elsewhere (Bernor et al., 1997) and was selected as a comparative standard for this study following previous work (e.g. Bernor et al., 2003b) as discussed in Chapter 3. The Höwenegg ellipse contrasts clearly with the other major well-sampled single population standard, the sample from La Roma 2. The Höwenegg and La Roma 2 95% confidence ellipses for siM3 and siM1 plot in contrasting quadrants in figure 6.13 with the MT III ellipses overlapping slightly (fig. 6.13A). The Höwenegg MP III's appear generally relatively short and relatively broad compared to the La Roma 2 standard. The Höwenegg hipparion is smaller than that from La Roma 2 (fig. 6.14) but appears in general to be larger than many other hipparions such as the smaller specimens from Pikermi. The mean habitat scores for the Höwenegg hipparion were -0.99 for MC III's and -0.74 for MT III's (as already noted).

Eppelsheim

The type locality for *Hippotherium primigenium* is the Eppelsheim in the fluviatile 'Dinotheriumsande' (=Sands with *Deinotherium*) of the Mainz Basin (Mainz, Germany). Two complete MP III's (one MT III and one MC III) from Eppelsheim were analyzed here and are plotted in figures 6.13 and 6.14. Both specimens appear broadly comparable in size and shape to the Höwenegg sample and plot within the Höwenegg 95% confidence ellipses for MGSV versus PC1 (fig. 6.14). One distinction between the Eppelsheim specimens and those from Höwenegg is in terms of siM3 (relative slenderness). The two specimens from Eppelsheim have lower values for siM3 and are relatively more slender than those from Höwenegg and plot below the Höwenegg 95% confidence ellipse for siM3 versus siM1 (fig. 6.13). The habitat scores for the two

Eppelsheim specimens were 0.09 (for the MC III HLMD3074 and 0.087 (for the MT III HLMD 3070).

Esselborn

Two MT III's from a second 'Dinotheriumsande' locality, Esselborn, were included in this analysis. Both specimens plotted squarely within the central portion of the Höwenegg 95% confidence ellipses for PC1 versus MGSV and siM3 versus siM1 (figs. 6.13A & 6.14A) and appear entirely like the Höwenegg MT III's in terms of overall size, relative elongation, and relative slenderness.. The resulting habitat scores for these two MT III's were -0.71 and -0.14.

Dorn-Dürkheim

A third locality of the Mainz Basin (albeit of a younger age) is the Turolian site of Dorn-Dürkheim 1. One MC III and two MT III's from Dorn-Dürkheim were analyzed here. The MC III, SMF-DD4435, is the type specimen of *Hippotherium kammerschmitti* KAISER ET AL. 2003. This specimen is smaller in size than MC III's from Höwenegg (fig. 6.14B). In terms of relative elongation and slenderness, SMF-DD4435 plots between the Höwenegg and La Roma 95% confidence ellipses for siM3 and siM1 and SMF-DD4435 is distinguished from the Höwenegg sample mostly by to greater relative slenderness (fig. 6.13B). The habitat score for SMF-DD4435 was -0.07.

The two complete MT III's from Dorn-Dürkheim shown in figures 6.13A and 6.14A contrast with SMF-DD4435 in both size and morphology. Both specimens plot within the Höwenegg 95% confidence ellipses for the plots of both PC1 versus MGSV and siM1 versus siM3. The habitat scores for these two MT III's were -1.73 and -0.30.

Charmoille

The locality of Charmoille (Ajoie, Switzerland) is part of the fluviatile deposits of the Elsgau also referred to as the 'Vogesensande' (Franzen & Storch, 1999) and five MP III's from Charmoille were available for this analysis (three MT III's and two MC III's). In general, the Charmoille MP III's are either smaller than the Höwenegg MP III's or comparable in size to the smallest of the Höwenegg MP III's (fig. 6.14) suggesting a hipparion population on average smaller than the Höwenegg hipparion but with an overlapping size range. In terms of relative slenderness and elongation, the Charmoille MP III's plot inside the Höwenegg 95% confidence ellipses for siM3 and siM1 (fig. 6.13). The two MC III's in particular have large values for siM3 indicating a very broad diaphysis (fig. 6.13B). This elevated value for siM3 is responsible for the very negative mean habitat score for these two MC III's of -1.53. The three MT III's from Charmoille resulted in a mean habitat score of -0.66.

Rudabánya

No specimens from Rudabánya (Hungary) were complete enough for the full analysis and computation of habitat scores. However, two MC III's and one MT III from Rudabánya did preserve the measurements M5, M1, and M3 which are plotted in figures 6.15 and 6.16. The MT III, MAFIV12038, is the type specimen for *Hippotherium intrans* KRETZOI 1983. This specimen appears elongate compared to the Höwenegg standard and comparable to the La Roma 2 hipparion in terms of elongation (fig. 6.15A). However, MAFIV12038 compared more closely to specimens from Höwenegg in terms of relative slenderness than to those from La Roma 2 (fig. 6.16A). With respect to size, MAFIV12038 appears comparable to the Höwenegg specimens (fig. 6.15A & 6.16A).

The MC III's plotted in figures 6.15B and 6.16B appear to represent a smaller hipparion than MAFIV12038 with MC III's similar in size to the sample from Baltavár

(Hungary). They appear to be elongate compared to the Baltavár and Höwenegg samples which seem to fit the same scaling trend and plot well above the Baltavár 95% confidence ellipse in figure 6.15B. However, these two MC III's do not appear relatively slender and plot within the Baltavár 95% confidence ellipse in terms of M3 versus M5 (fig. 6.16B).

While habitat scores could not be computed for these specimens, they were estimated based on estimated values for MGSV. MGSV was estimated using a least squares regression of MGSV versus M5. The resulting estimated habitat scores were -1.36 for the MT III MAFIV12038 and -1.47 and -1.22 for the two MC III's.

Inzersdorf

Like Rudabánya, Inzersdorf (Austria) in the Vienna Basin is a part of the fluviolacustric deposits of the Pannonian lake system (Steininger et al., 1996; Franzen & Storch, 1999). Eight MP III's were available from Inzersdorf for study here: four MT III's and four MC III's. Collectively, these eight specimens suggest a hipparion most similar to that from Charmoille in size: on average smaller than Höwenegg but overlapping in size range (fig. 6.14). The Inzersdorf specimens generally plot within the Höwenegg 95% confidence ellipse in terms of siM3 and siM1 (fig. 6.18). Three of the Inzersdorf MT III's and two of the Inzersdorf MC III's plot inside the Baltavár 95% confidence ellipse for siM3 versus siM1 (fig. 6.18) and all of the Inzersdorf specimens are consistent with the Baltavár specimens as far as size (fig. 7.17). The Inzersdorf specimens are also clearly not as elongate as specimens from Rudabánya (fig. 6.15). The mean habitat scores for the Inzersdorf hipparion were -0.58 based on MC III's and -1.06 based on MT III's.

Prottes

One MT III (NHMW9101) was analyzed from the Vienna Basin locality of Prottes. This specimen plots at the margin of the Höwenegg 95% confidence ellipse for PC1 versus MGSV (fig. 6.17A) and inside the Höwenegg 95% confidence ellipse for siM3 versus siM1 (fig. 6.18A). The Prottes specimen is also inside the Baltavár 95% confidence ellipses in figures 6.17A and 6.18A. Overall, the Prottes specimen appears to compare favorably with the Inzersdorf MP III's. The habitat score for NHMW9101 was -0.06.

Gols

Two MC III's from Gols (also in the Vienna Basin) are shown in figures 6.17B and 6.18B and appear to contrast in size and morphology. One of these (NHMW1383/1) is smaller than the Höwenegg hipparion, elongate, and relatively broad in the diaphysis (figs. 6.17B & 6.18B). This specimen appears to compare favorably with small, elongate but broad MC III's from Rudabánya (figs. 6.15B & 6.16B). The second Gols MC III (NHMW1383/1) is larger in size and is also relatively more slender (figs. 6.17B & 6.18B). The habitat score for the smaller and elongate Gols MC III (NHMW1383/1) was -0.65. The larger Gols MC III (NHMW1383/3) had a habitat score of 0.49.

Schwechat

The single MC III from Schwechat (Vienna Basin, Austria) plots with the Inzersdorf specimens in terms of size and slenderness but is somewhat more elongate (figs. 6.17B & 6.18B). The habitat score for this specimen was -0.28.

Sümeg

The single complete MC III (MAFIV13242) from Sümeg (Hungary), a karst fissure locality of the Pannonian Basin, is the type specimen for *Hippotherium sumegense*

KRETZOI 1984. MAFIV13242 is smaller that MC III's from Höwenegg and similar in size to those from Baltavár (fig. 6.17B). It is also relatively short and broad and plots to the left of Höwenegg and Baltavár 95% confidence ellipses for siM3 versus siM1 (fig. 6.18B). The habitat score for this specimen was -1.31.

Csákvár

Two MT III's and three MC III's from Csákvár (Hungary) are plotted in figures 6.17 and 6.18. These specimens appear on average larger than MP III's from Inzersdorf and most comparable to MP III's from Höwenegg in terms of size (fig. 6.17). The two MT III's from Csákvár plot within the Höwenegg 95% confidence ellipse for siM3 versus siM1 (fig. 6.18). The three Csákvár MC III's appear particularly variable in terms of relative elongation. The two smallest Csákvár MC III's have positive values for siM1 (relative elongation) comparable to those for the La Roma 2 MC III's. Of these, MAFIV 4283C appears particularly elongate and compares closely with NHMW1383/1 from Gols.

Three additional MT III's from Csákvár preserved M5 and M1 and these specimens are added to figure 6.15A. Two of these appear to be relatively elongate and compare closely with the type of *Hippotherium intrans* from Rudabánya. It appears reasonable to partition the Csákvár sample into two parts: a group of more elongate MP III's and a group of less elongate MP III's. The first group of elongate MP III's would include the complete and well-preserved MC III, MAFIV 4283C, with a very elevated value for siM1 and two less complete MT III's shown in 6.15A. This group is referred to as the Csákvár Elongate Morph.

The remaining MP III's from Csákvár are less elongate and are assigned to the Csákvár Shortened Morph. These specimens appear to compare favorably with the Höwenegg MP III's.

The habitat score for MAFIV 4283C representing the Csákvár Elongate Morph was -0.65. The mean habitat scores for the Csákvár Shortened Morph were 0.14 (based on two MC III's) and -0.40 (based on two MT III's).

Polgárdi

Four MP III's from Polgárdi (Hungary) compare closely with the Höwenegg standard in terms of size and relative elongation (figs. 6.17 & 6.18). The main contrast with the Höwenegg MP III's is in terms of somewhat greater relative slenderness (fig. 6.18). The closest comparisons for the four Polgárdi MP III's appear to be the Inzersdorf MP III's which tend to be smaller and the Csákvár Shortened Morph MP III's which tend to be broader. The mean habitat scores for the Polgárdi hipparion were 0.10 based on MC III's and 0.04 based on MT III's.

Baltavár

The Baltavár sample of MP III's is large enough that 95% confidence ellipses were calculated for the Baltavár MP III's shown in figures 6.17 and 6.18. Overall, the 95% confidence ellipses for the Baltavár MP III's appear comparable to those from Höwenegg and La Roma 2 in terms of how tightly they constrain specimens. The Baltavár MP III's appear more variable than those from Höwenegg in terms of overall size but less variable in terms of the shape variables of relative elongation and relative slenderness (figs. 6.17 & 6.18). This result is consistent with a single species at Baltavár.

A careful consideration of the Baltavár sample, however, suggests that a second rare species is likely. The MT III MAFI Ob 3209/1 is a distinct outlier from the other Baltavár MT III's and has a length measurement of 252 mm. The next longest Baltavár MT III has a length measurement of 233.5 mm. Even if MAFI Ob 3209/1 is accommodated in a single hipparion species from Baltavár, a very small MC III from the

Savari Museum (Savari 54.387.1) had a length measurement of only 187.5 mm (the next shortest MC III had a length measurement of 194.5 mm) and it would seem unlikely that this specimen derived from the same species as MAFI Ob 3209/1. Only the M10 and M1 measurements were available for Savari 54.387.1 and it could not be plotted in figures 6.17 and 6.18. Consideration of the two outliers, MAFI Ob 3209/1 and Savari 54.387.1, in conjunction with the rest of the Baltavár sample suggests the presence of one common species smaller in size than the Höwenegg hipparion and one rare species represented by MAFI Ob 3209/1.

MAFI Ob 3209/1 compares favorably with Csákvár specimens of the Csákvár Shortened Morph. The other MP III's from Baltavár are similar in shape to the Höwenegg MP III's although the Baltavár MC III's appear on average relatively shorter and more slender than the Höwenegg MC III's (fig. 6.18B).

The mean habitat scores for the Baltavár MP III's excluding MAFI Ob 3209/1 were -0.42 (for MC III's) and -0.09 (for MT III's). The MT III MAFI Ob 3209/1 had a habitat score of -0.68.

Kislang

A single MT III from the much younger (= MN 16) Hungarian locality of Kislang was included here and had a habitat score of 1.06. The Kislang MT III plots within the La Roma 2 95% confidence ellipse in both figures 6.17 and 6.18 and represents a large hipparion with elongate and slender MP III's.

Mont Luberon

Four MC III's and seven MT III's from Mont Luberon (France) are plotted in figures 6.19 and 6.20 with specimens attributed to *Cremohipparion mediterraneum* from Pikermi (Greece) and *Cormohipparion sinapensis* from Sinap (Turkey) as well as the

sample of MP III's from Inzersdorf. The Mont Luberon specimens are smaller than specimens from Höwenegg and comparable in size to *Cremohipparion mediterraneum* and the Inzersdorf sample (fig. 6.19). The Mont Luberon MT III's are elongate compared to those from Inzersdorf and compare very nearly with the MT III's of *Cremohipparion mediterraneum* with regards to relative elongation and slenderness (fig. 6.20A). The Mont Luberon MC III's do not appear as elongate as those of *Cremohipparion mediterraneum* and are more similar to *Cormohipparion sinapensis* in terms of relative length (fig. 6.20B).

The Mont Luberon MT III's are somewhat variable and three of them appear smaller and relatively more elongate (figs. 6.19A & 6.20A) Thus, there are some grounds to suggest more than one species at Mont Luberon. However, pending further study, the Mont Luberon MP III's are considered as a single species here. The mean habitat score for the Mont Luberon MT III's was 0.71. MC III's from Mont Luberon resulted in a habitat score of 0.25.

Fossil hipparionines of Turkey, Iran, Afghanistan, Kazakhstan, and Pakistan

Sinap Formation

The diverse sample of hipparion MP III's from the Sinap Formation (Turkey) has recently been treated extensively in conjunction with craniodental material (Bernor et al., 2003b). The results for MP III's from the Sinap Formation are shown here in figures 6.21 and 6.22 according to these recent classifications (see Tables 11.11 and 11.12 in Bernor et al., 2003b).

In terms of overall size, the Sinap MP III's appear to mainly belong to hipparions smaller than the Höwenegg hipparion or in the bottom part of the Höwenegg size range (fig. 6.21). The smallest of the Sinap hipparions appears to be *"Hipparion" uzunagizli*

and a small hipparion from Sinap Locality 42 represented by AS94/1293 (fig. 6.21A). *"Hipparion" uzunagizli* appears to have a relatively slender diaphysis and is elongate compared to *"Hipparion" kecigibi* (fig. 6.22).

Three species of hipparion appear larger than *"Hipparion" uzunagizli*. These are *"Hipparion" kecigibi*, *Cormohipparion sinapensis*, and a species described as cursorial by Bernor et al. (2003b) (fig. 6.21). *"Hipparion" kecigibi* is comparable to the Höwenegg standard in diaphysis breadth but appears on average relatively shorter and generally plots in the left portion of the Höwenegg 95% confidence ellipse for siM3 versus siM1 (fig. 6.22). *Cormohipparion sinapensis* is more elongate than *"Hipparion" kecigibi* and the cursorial form of Bernor et al. (2003b) is generally more slender than *Cormohipparion sinapensis* (fig. 6.22).

The mean habitat scores for *"Hipparion" kecigibi* were -0.83 (based on MT III's) and -0.45 (based on MC III's). Mean habitat scores for *"Hipparion" uzunagizli* were 0.89 and 0.98 based on MT III's and MC III's respectively. *Cormohipparion sinapensis* yielded mean habitat scores of -0.53 (for MT III's) and -0.30 (for MC III's). MP III's of the fourth form described as cursorial (Bernor et al., 2003b) had mean habitat scores of 0.27 (for MT III's) and 0.60 (for MC III's).

Esme Akçaköy

Seven MT III's and four MC III's from Esme Akçaköy are shown in figures 6.21 and 6.22. The 95% confidence ellipse for the MT III sample from Esme Akçaköy is shown in both plots (figs. 6.21A & 6.22A) and suggests variability in MT III's comparable to that at Höwenegg and La Roma 2 and consistent with a single species of hipparion. The four MC III's from Esme Akçaköy also plot near one another and are consistent with a single species hypothesis for Esme Akçaköy.

The Esme Akçaköy MT III's appear to overlap with the Höwenegg MP III's in terms of size, relative slenderness, and relative elongation. Individual MT III's from Esme Akçaköy would not be distinguishable from the Höwenegg standard on their own. However, collectively the Esme Akçaköy sample of MT III's describes a species of hipparion on average smaller than the Höwenegg hipparion with what are on average more slender and elongate MT III's (figs. 6.21A & 6.22A). Notably the Esme Akçaköy 95% confidence ellipses for PC1 versus MGSV and siM3 versus siM1 enclose all MT III's attributed to *Cormohipparion sinapensis* (figs. 6.21A & 6.22A).

The four MC III's from Esme Akçaköy contrast with specimens attributed to *Cormohipparion sinapensis* in size and relative slenderness (figs. 6.21B & 6.22B). The Esme Akçaköy MC III's are relatively more slender than those of *Cormohipparion sinapensis* (= the 'Esme Akçaköy effect' of Bernor et al., 2003b). The mean habitat scores for the Esme Akçaköy MP III's were -0.12 based on MT III's and 0.27 based on MC III's.

Akkaşdağı

The Akkaşdağı hipparions are discussed thoroughly elsewhere (Koufos & Vlachou, in press; Scott & Maga, in press) and the species level assignments used there are replicated here. The generic designation for these taxa follows that in Bernor et al. (1996b).

Three general body size ranges are represented at Akkaşdağı (fig. 6.23). MP III's referred to *Cremohipparion moldavicum* are smaller in size than *Hippotherium primigenium* from Höwenegg. *Hipparion* cf. *dietrichi* and "*?Plesiohipparion*" cf. *"?Plesiohipparion"* cf. *longipes* compare very closely in size to *Hippotherium primigenium* from Höwenegg. "*Hippotherium*" cf. *brachypus* is larger than *Hippotherium primigenium* from Höwenegg.

Cremohipparion moldavicum and *Hipparion* cf. *dietrichi* are similar in terms of MP III relative elongation and relative slenderness. Both have relatively elongate and slender MC III's and relatively elongate MT III's compared to the Höwenegg hipparion (fig. 6.24). "*?Plesiohipparion*" cf. *longipes* has extremely elongate and slender MP III's that are relatively long compared even to the La Roma 2 standard (fig. 6.24). "*Hippotherium*" cf. *brachypus* has MT III's that plot within the Höwenegg 95% confidence ellipses for elongation and slenderness (siM3 versus siM1) (fig. 6.24A). However, the "*Hippotherium*" cf. *brachypus* MC III's appear relatively more slender than those of *Hippotherium primigenium* from Höwenegg (fig. 6.24B).

The mean habitat scores for all four Akkaşdağı species are positive. "*Hippotherium*" cf. *brachypus* has the lowest mean habitat scores: 0.36 and 0.14 respectively for MC III's and MT III's. "*?Plesiohipparion*" cf. *longipes* has extremely positive mean habitat scores of 1.19 based on MC III's and 0.79 based on MT III's. MP III's of *Cremohipparion moldavicum* and *Hipparion* cf. *dietrichi* resulted in intermediate positive mean habitat scores: 0.51 (based on MC III's) and 0.29 (based on MT III's) for *Cremohipparion moldavicum* and 0.36 (based on MC III's) and 0.64 (based on MT III's) for *Hipparion* cf. *dietrichi*.

Çalta

Çalta (Turkey) is younger in age (= MN 15) (Mein, 1990) than Akkaşdağı and most localities discussed here but includes MP III's that are extreme morphologically. Two Çalta MT III's are larger than the Höwenegg MT III's and are also relatively shorter (figs. 6.23A & 6.24A). A third MT III from Çalta shows the opposite morphology and is extremely elongate – relatively longer than La Roma 2 sample of MT III's and the "*?Plesiohipparion*" cf. *longipes* MT III's from Akkaşdağı (fig. 6.24A). It is similar in

size (as measured by MGSV) to the Höwenegg hipparion (fig. 6.23A) and can also be considered broad across the diaphysis (fig. 6.24A).

The five MC III's studied from Çalta clearly belong to the same species as the short and large MT III's from Çalta. They are large and relatively short compared to the Höwenegg standard and most of the La Roma 2 MC III's (figs. 23A & 24B). One of these a MC III's, ACA49a, is the type of *Hipparion heintzi* EISENMANN & SONDAAR 1998.

The mean habitat score for the five MC III's from Çalta was 0.16. The two shortened MT III's from Çalta had negative habitat scores of -0.56 and -0.06. The relatively elongate MT III from Çalta had a habitat score of 0.50.

Siwaliks

The range of variation in size for Siwaliks specimens studied here appears large. Eight MT III's plotted from below the Höwenegg size range to above the La Roma 2 size range as measured by MGSV (fig. 6.25A). The two MC III's also appear to differ in terms of size (fig. 6.25B).

The size variation observed for the Siwalik specimens appears to be matched by morphological variation in relative slenderness and elongation. All four of the smaller Siwalik MT III's appear to belong to a species that has relatively more elongate and on average relatively more slender MP III's fig. 6.26A).. The smaller MC III also appears relatively slender and elongate (fig. 6.26B). The mean habitat score for the four elongate and slender MT III's was 0.35. The single MC III is probably conspecific with these MT III's had a habitat score of 0.58.

Four larger MT III's were relatively short and broad (fig. 6.26A). The other Siwalik MC III in this study is also relatively short although it is slender compared to the Höwenegg standard (fig. 6.26B). The mean habitat score for this group of MT III's was -

0.91. The shortened (but slender) MC III is a possible conspecific of these MT III's but due to it's relative slenderness it had a positive habitat score of 0.32.

Two other MT III's shown in figures 6.25A and 6.26A are quite large in size. These two MT III's plotted at the opposite ends of the Höwenegg 95% confidence ellipse in terms of siM3 and siM1 suggesting that they either represent opposite extremes of variation for a third larger species or individuals of two separate species. In the later case, the less elongate and slender of these two (GSP 17774) would likely be a large individual belonging to the form described above already represented by four large, short, and broad MT III's. The more elongate and slender of these two MT III's (GSP 50353) could represent a third species. Habitat scores for these specimens were -1.76 for GSP 17774 and 0.44 for GSP 50353.

Molayan

Five MT III's from Molayan (Afghanistan) are shown in figures 6.25A and 6.26A. These specimens appear consistent with placement in a single species and appear to represent a hipparion smaller in size that that from Höwenegg with very elongate MT III's that are not relatively slender (figs. 6.25A & 6.26A). Thus, despite the extreme elongation observed here the mean habitat score for these specimens was -0.34.

Maragheh

A large sample of MP III's from Maragheh was analyzed here and included 25 MC III's and 15 MT III's that were complete and well-preserved enough to calculate MGSV. These specimens have been sorted into groups on the basis of size and morphology and every attempt was made to minimize the number of groups.

The MC III's have been divided into five groups and two of these include several MC III's allowing for the calculation of 95% confidence ellipses in figures 6.27B and

6.28B. The first group of Maragheh MC III's can be distinguished by their small size and it includes four MC III's (fig. 6.27B). These specimens are designated as the Margheh Dwarf Morph and are generally elongate but vary in terms of relative slenderness (fig. 6.28B). The mean habitat score for MC III's assigned to the Margheh Dwarf Morph was 0.31.

Seven MC III's have been assigned to the Maragheh Small Morph. These specimens form a cluster below the Höwenegg 95% confidence ellipse for siM3 versus siM1 in figure 6.28B. They are slender and smaller than the Höwenegg hipparion in size but larger than the Maragheh Dwarf Morph (figs. 6.27B & 6.28B). The mean habitat score for these MC III's was 0.33.

Ten other MC III's are larger than the Maragheh Small Morph MC III's and are also relatively more elongate (figs. 6.27B & 6.28B). These have been designated as the Maragheh Elongate Morph and their 95% confidence ellipses for PC1 versus MGSV and siM3 versus siM1 are shown in figures 6.27B and 6.28B. While the Maragheh Small Morph MC III's are clearly derived from a hipparion smaller than *Hippotherium primigenium* from Höwenegg, the size range for the Maragheh Elongate Morph is similar to that of *Hippotherium primigenium* from Höwenegg. The ranges of siM1 for the Maragheh Small Morph and the Maragheh Elongate Morph do not overlap. The four much smaller MC III's assigned to the Maragheh Dwarf Morph appear to be intermediate in terms of relative elongation compared to the Maragheh Small Morph and the Maragheh Elongate Morph (fig. 6.28B). The 95% confidence ellipse of siM3 versus siM1 for the ten MC III's of the Maragheh Elongate Morph is quite large compared to those for the Höwenegg and La Roma 2 standards. This appears to be driven by a single outlier - MAR39 (MNHN collection). This outlier is the largest specimen attributed to the Maragheh Elongate Morph as well as the one with the largest value for siM3. However,

only Maragheh Elongate Morph MC III's have values for siM1 comparable with that of MAR39. It is possible that MAR39 is a single representative of another species of an older or younger population of the same species represented by the other Margheh Elongate Morph MC III's. All ten Maragheh Elongate Morph MC III's together resulted in a mean habitat score of 0.83.

The four remaining Maragheh MC III's are of two sizes. Two specimens are similar in size to the Maragheh Small Morph and two specimens are larger than the Maragheh Elongate Morph and most similar in size to larger MC III's from Höwenegg (fig. 6.27B). The two smaller specimens are distinguished by greater relative breadth and are grouped together as the Maragheh Broad Morph (fig. 6.28B). Their mean habitat score was -1.38. The two larger specimens are similar in size and plot within and on the border of the Höwenegg 95% confidence ellipse for PC1 versus MGSV (fig. 6.27B). One of the larger specimens is relatively slender while the other is relatively broad (fig. 6.28B). These two larger but morphologically different specimens are lumped in the Maragheh Large Morph here but are potentially candidates for separate species. The habitat scores for the two Maragheh Large Morph MC III's were widely divergent: -0.99 and 1.12.

The fifteen complete MT III's from Maragheh analyzed here are not as variable in morphology (fig. 6.28)) as the MC III's but do vary to a similar degree in terms of size (fig. 6.27). Thus, the MT III's from Maragheh were matched to the Morphs defined based on MC III's primarily on the basis of size (see fig. 6.27A). Thus, the three smallest MT III's are assigned to the Margheh Dwarf Morph. Three other MT III's are assigned to the Maragheh Small Morph. Eight MT III's are placed in the Maragheh Elongate Morph. The largest MT III is relatively short and is best matched with the Margheh Large Morph. The mean habitat scores for Maragheh MT III's were 1.33, 0.33, 0.72, and -0.33 respectively

for the Margheh Dwarf Morph, Maragheh Small Morph, Maragheh Elongate Morph, and the Maragheh Large Morph.

Kalmakpai

The MT III of *Hipparion* cf. *elegans* (Eisenmann & Mein, 1996) from the MN 13 locality of Kalmakpai (Kazakhstan) resulted in a habitat score of 1.02. This specimen is clearly relatively elongate and slender and plots to the right of the La Roma 2 95% confidence ellipse in figure 6.26A. With respect to overall size, the Kalmakpai MT III appears comparable to the smaller MT III's of *Hippotherium primigenium* from Höwenegg (fig. 6.25A).

Fossil hipparionines of Africa

Bou Hanifia

Three MT III's from Bou Hanifia (Algeria) plot in a cluster around the zone of overlap between the 95% confidence ellipses of the Höwenegg and La Roma 2 standards for siM3 versus siM1 (fig. 6.29A). They appear to be moderately elongate and moderately slender. These three specimens also appear to derive from a species smaller than *Hippotherium primigenium* from Höwenegg (6.30A). The mean habitat score for the Bou Hanifia MT III's was 0.17.

Sahabi

One complete MC III from Sahabi, ISP27P25B, assigned to *Cremohipparion* aff. *matthewi* (Bernor & Scott, 2003) is plotted in figure 6.29B and 6.30B. This specimen is clearly relatively slender but does not appear to be elongate for its size. The habitat score for ISP27P25B was 1.07.

Lothagam

Two MC III's from Lothagam plot in contrasting quadrants in figure 6.29B. One is elongate and slender and the other is short and broad. The short broad MC III (= KNM-LT22871) is quite large – larger than the La Roma 2 MC III's (fig. 6.30B). The slender elongate specimen (= KNM-LT139A) is quite small – like the smallest of the Höwenegg MC III's in terms of MGSV. The habitat scores for these two specimens were -0.71 (KNM-LT22871) and 1.00 (KNM-LT139A).

One MT III from Lothagam (KNM-LT25470) matches the short broad MC III in terms of large size and is also relatively short (although somewhat slender). The habitat score for KNM-LT25470 was 0.13.

Fossil hipparionines of North America

Christmas Quarry

The sample of MP III's from Christmas Quarry is diverse in morphology and size and is plotted in figures 6.31 and 6.32. These specimens have been included primarily as additional data points for the description of hipparionine MP III scaling and to demonstrate the range of MP III morphologies possible for an early hipparion immigrant to the Old World. A full discussion of this sample is beyond the scope of this thesis.

The midsized specimens attributed to the *Cormohipparion occidentale* group are shown separately and specimens of *Cormohipparion sinapensis* from the Sinap Formation have also been plotted in figures 6.31 and 6.32. These two groups of MP III's appear broadly comparable.

DISCUSSION

The validity and usefulness of the habitat scores computed here are discussed below and followed by discussions of hipparions from the various sites included in this

study grouped by general region (these regions are an organizational convenience and are not meant to imply biogeographic similarity). Likely species groupings were determined based on: 1) the literature, 2) variation in MP III size at various sites, and 3) on the basis of MP III morphology. The rationale for species level identifications is reported in various sections below. This likely species level taxonomy allows habitat score summaries by species and site and provides a basis for paleoenvironmental interpretations for each site. The generic names used for species as discussed here follow the scheme of Bernor et al. (1996b) which may differ from the usage of earlier authors (often generic designations were simply *Hipparion*). A final section below includes a discussion of probable conspecifics from different sites for those species that are better sampled and remarks concerning general trends discernable across sites.

Habitat score validity

The habitat scores generated here based on both the MT III and MC III appear likely to track the spectrum from open to closed habitats quite generally and appear applicable to bovids, equines, and hipparionines. The habitat score appears to meet all five criteria suggested *a priori* for such a variable (see Chapter 3).

First, it clearly separates bovids of known habitats. This includes separating forest and plains bovids which were used to generate the habitat score coefficients and, at least in the case of the metatarsal, the habitat score also separates heavy cover and light cover bovids which were not used to generate the habitat score coefficients (fig. 6.1). Heavy cover bovids plot to the left of light cover bovids and, in the case of the metatarsals, this difference was significant. This result is supportive of the utility of the habitat score since the light cover and heavy cover species were not included in the generation of the formula for habitat score.

Second, the habitat score separates living equines (see Chapter 5). For example, *Equus burchelli* and *Equus grevyi* are separated by habitat score. While both species are tied to open habitats, *Equus grevyi* is more constrained to arid and very open habitats (Estes, 1991). In contrast, *Equus burchelli* is more like a light cover bovid using open woodlands and requiring wetter habitats (Estes, 1991). The most important result here is where *Equus burchelli* and *Equus grevyi* plot relative to each other and not what their absolute scores are compared to bovids. *Equus burchelli* plots to the left of *Equus grevyi* in terms of habitat score (see Chapter 5) as would be predicted based on what differences there are in habitat usage for these two species. An extant forest dwelling equine would be expected to plot to the left of the left of *Equus burchelli*.

Third, the habitat score separates the Höwenegg sample from other hipparionines such as the La Roma hipparionine. The interpretation of the Höwenegg hipparion as a forest dweller is robust (Bernor et al., 1988; Bernor et al., 1997; Kaiser, 2003) and La Roma 2 hipparion would appear to be more open-adapted (Alcalá, 1994). Once again, the more closed form (the Höwenegg hipparion) has the lower habitat score (fig. 6.33, see also tab. 6.4).

Fourth, the separation of bovids, equines, and hipparionines from different habitats is in conformity with the biomechanical predictions made regarding morphology and habitat. Scores for open habitat forms result from elongation and slenderness of the metapodials.

Finally, the separation of bovids, hipparionines, and equines by habitat is such that closed forms all have low scores relative to open forms for all three groups. While grade shifts are possible and even likely between different taxonomic groups, within each group the more closed forms have lower habitat scores and plot to the left of more open adapted species. This same pattern can be seen within the Bovidae when species are

subdivided by subfamily (fig. 6.1). It would appear that there is a strong case for the validity of the habitat score described here for distinguishing between species that are relatively more open habitat or closed habitat adapted.

It is also worth noting that there is a strong correlation between PC1 and habitat score ($p<0.0001$, see fig. 6.34). The main differences between habitat score and PC1 is that habitat score gives a much stronger weight to relative slenderness than PC1 and PC1 is based on additional variables besides siM1 and siM3. Both habitat score and PC1 are potential candidates for strong correlates of habitat type. The bovid analogy is considered robust here and therefore habitat score has been given primacy over PC1 in the interpretations discussed below. However, PC1 is an alternative measure likely applicable to habitat and it is summarized in table 6.5 by site and species.

Fossil hipparionines from Spain

Los Valles de Fuentidueña

The type specimen for *Hipparion melendezi* ALBERDI 1974 is an MT III from Los Valles de Fuentidueña (MN 9) (Alberdi, 1974; Alberdi, 1981). A single species of hipparionine, *Hipparion* cf. *concudense* PIRLOT 1956, is recorded for Los Valles de Fuentidueña in the NOW mammal database (Neogene of the Old World: Database of fossil mammals, n.d.) and implies possible synonymy with *Hipparion concudense* from Concud. A skull from the nearby site of El Lugarejo attributed to *Hipparion melendezi* (Alberdi, 1974) suggests that *Hipparion melendezi* is part of *Hipparion* s.s.-Group (Bernor et al., 1989; Bernor et al., 1996b).

The results of the morphometric analyses of MP III's from Los Valles de Fuentidueña suggested only a single species of hipparion. Specimens from Concud (the type locality for *Hipparion concudense* PIRLOT 1956) could derive from multiple species

and appear less slender and elongate than those from Los Valles de Fuentidueña (fig. 6.2). The Concud MT III's are all outside of the La Roma 95% confidence ellipse and the Los Valles de Fuentidueña MT III's are all within the La Roma 95% confidence ellipse. Thus, on the basis of MP III morphology the Los Valles de Fuentidueña hipparion appears distinct from *Hipparion concudense*. The best taxonomic attribution for the Los Valles de Fuentidueña hipparion would be *Hipparion melendezi* following Alberdi (1974; 1981).

Alberdi et al. (1981) noted that hipparionines dominated the Los Valles de Fuentidueña fossil assemblage contributing 75% of the specimens in the assemblage followed by rhinocerotids (8.24%) and giraffids (5.7%). Alberdi (1981) reported 2,108 specimens of *Hipparion* from Los Valles de Fuentidueña. Morales and Soria (1981) identified 586 artiodactyls from Los Valles de Fuentidueña of which 386 were identified as the giraffid, *Decennatherium pachecoi*, and 108 were identified as the tragulid, *Dorcatherium naui*. Bovids are rare at Los Valles de Fuentidueña; only 23 specimens were identified as bovids (*Miotragocerus* sp.) by Morales and Soria (1981). The artiodactyls from Los Valles de Fuentidueña are categorized as browsers (NOW, n.d.). In contrast, *Hipparion melendezi* is identified as a probable grazer (NOW, n.d.). It would appear the Los Valles de Fuentidueña represents a community dominated by a grazing equid while artiodactyls (mostly giraffids and tragulids) exploited a less common browsing niche.

The hypothesis that *Hipparion melendezi* from Los Valles de Fuentidueña may represent an MN 9 grazing hipparionine is supported by its habitat scores. The mean habitat score for MT III's was 0.74 which contrasts sharply with that of -0.74 for *Hippotherium primigenium* from Höwenegg which is considered a browsing inhabitant of subtropical mesophytic forest (Bernor et al., 1988; Bernor et al., 1997; Kaiser, 2003).

This contrast with Höwenegg in terms of habitat score suggests a habitat preference for more open country.

El Lugarejo

Like Los Valles de Fuentidueña, El Lugarejo (Avila, Spain) is a MN 9 locality in the Duero Basin (Morales et al., 1981; NOW, n.d.). Thus, temporally and geographically these two sites are close. The El Lugarejo MP III's were not as numerous as those from Los Valles de Fuentidueña but they compare favorably with them. Slightly smaller body size is possible for the El Lugarejo hipparion but conspecific status with *Hipparion melendezi* from Los Valles de Fuentidueña would seem reasonable. Splitting the temporally, geographically, and morphologically close specimens from El Lugarejo would serve no other purpose than to confuse discussion. A skull from El Lugarejo is attributed to *Hipparion melendezi* (Alberdi, 1974).

The habitat scores for the El Lugarejo specimens are 0.27 and 0.62 for two MC III's and 0.40 for one MT III. Combining the El Lugarejo and Los Valles de Fuentidueña samples to determine mean habitat scores for *Hipparion melendezi* were 0.67 for MT III's (N = 5) and 0.61 for MC III's (N = 3). These scores suggest a habitat preference for open country by *Hipparion melendezi* and the likely presence of a large grazing niche in the Duero Basin during MN 9.

Santiga

The site of Santiga near Sabadell, Spain is assigned to the *Cricetulodon* Zone of MN 9 (Agusti, 1982) and appears comparable in age to Can Ponsic and Ballestar and is possibly slightly older than Can Llobateres at the top of the *Cricetulodon* Zone.

Crusafont and Golpe (1972) referred the hipparion specimens from Santiga to *Hipparion catalaunicum*. PIRLOT 1956 described from Hostalets de Pierola. Pirlot (1956)

identifies specimens from La Tarumba and Can Llobateres as likely representatives of *Hipparion catalaunicum*. However, the Santiga MP III's discussed here are smaller and relatively shorter than specimens from La Tarumba and Can Llobateres (figs. 6.2 & 6.3). *Hipparion catalaunicum* would appear to be best reserved for specimens from La Tarumba and Can Llobateres.

Forsten (1997) suggested that Santiga preserved two species of hipparionine: 1) a medium-sized to small form to which most specimens can be attributed, and 2) a rare large former represented by an astragalus, a fragmentary calcaneum, a few isolated teeth. The assignment of Santiga MP III's all to a single smaller species by Forsten (1997) is in agreement with the results of this analysis.

Forsten (1997) compared the Santiga MP III's favorably with those from Piera (Spain) and Montredon (Herault, France) and suggested that a simple increase in size was most likely from Santiga to Piera. The results here suggest morphological as well as size differences between the Santiga and Piera MP III samples. The Piera and Santiga MC III's overlap in terms of siM3 (relative diaphysis breadth) but are clearly distinct in terms of relative length (siM1) and size (MGSV) (see figs. 6.2 & 6.3). Forsten (1997) also found a greater plication count and longer protocone for the Santiga hipparions compared to those from Piera.

Montredon is the type locality for *"?Hippotherium" depereti* SONDAAR 1974 which Bernor et al. (1996b) places in the *Hippotherium primigenium* Complex on the basis of robust metapodials and rich cheek tooth enamel plication. The Montredon and Santiga samples are described as comparable in terms of MP III morphology, protoconal length, and plication count while the Montredon sample may represent a slightly larger form (Forsten, 1997).

A single skull is known from Santiga but is not figured in Forsten (1997). The preorbital fossa (POF) for this specimen is described as large, posteriorly pocketed and distinct anteriorly but without an anterior rim. The large POF and posterior pocketing are consistent with assignment to the *Hippotherium primigenium* Group. The description of the POF for the Santiga skull appears similar to that of *"Hipparion" kecigibi* BERNOR ET AL. 2003 from the Sinap Formation in Turkey to which short and broad MP III's have also been attributed (Bernor et al., 2003b). According to Bernor et al. (2003b), the POF of *"Hipparion" kecigibi* is "subtriangular shaped and anteroposteriorly oriented, deeply pockets posteriorly, medially deep, with moderately delineated peripheral border outline and no anterior rim."

While further study is clearly needed, it would appear that a close phylogenetic relationship between three forms with short and broad MP III's - *"?Hippotherium" depereti*, the Santiga hipparion, and *"Hipparion" kecigibi* - is possible. The morphology described for the Santiga specimens appears consistent with membership in the *Hippotherium primigenium* Complex but a conservative approach is to refer to the Santiga MP III's as *"Hipparion"* cf. *depereti* and to the Montredon material as *"Hipparion" depereti*.

The habitat scores for *"Hipparion"* cf. *depereti* from Santiga are among the most negative for the entire sample (mean scores of -1.01 for MC III's and -1.06 for MT III's). For example, only *Hippotherium sumegense* (N=1) and the Charmoille hipparion (N=2) had lower habitat scores for MC III. These very negative habitat scores suggest forested habitats or upland habitats replete with difficult terrain for *"Hipparion"* cf. *depereti*.

If a second rarer larger species was in fact present at Santiga, its rarity makes it less significant as a habitat indicator. However, the possibility of two species at Santiga should be discussed when hipparionine diversity is compared across sites.

Can Llobateres

With a paleomagnetic correlation of C4Ar and MN 9 mammal correlation (Agusti et al., 1997; Agusti et al., 2001), Can Llobateres in the Valles-Penedes Basin is likely very near the MN 9/10 boundary. The fauna at Can Llobateres also includes the hominoid, *Dryopithecus laietanus* (Moyà-Solà & Köhler, 1996).

The hipparions of Can Llobateres were attributed to *Hipparion catalaunicum* by Pirlot (1956) which has been included in the *Hippotherium primigenium* Complex as *"Hippotherium" catalaunicum* (Bernor et al., 1996b). However, the results reported here suggest two species of hipparion at Can Llobateres: a smaller species and a species with slender MC III's similar in size to *Hippotherium primigenium* from Höwenegg.

"Hippotherium" catalaunicum is derived in comparison to *Hippotherium primigenium* in having a very elongate and anteroposteriorly oriented POF (Woodburne & Bernor, 1980; Bernor et al., 1996b). A close relationship was hypothesized between *"Hippotherium" catalaunicum* and the Piera hipparion (referred to as *"Hippotherium"* aff. *catalaunicum*) which retains a POF of similar length and orientation to that of *"Hippotherium" catalaunicum* (Bernor et al., 1996b). Similar, POF morphology was reported for *"Hippotherium" africanum* ARAMBOURG 1959 and advanced as evidence for a *"Hippotherium" catalaunicum*-*"Hippotherium" africanum* clade. Thus, MP III's which are from Can Llobateres may be productively compared with those of *Hippotherium primigenium*, *"Hippotherium" africanum*, and the sample from Piera.

Three well-preserved MT III specimens of *"Hippotherium" africanum* from Bou Hanifia which were considered relatively more elongate and slender than *Hippotherium primigenium* from Höwenegg (Bernor & Scott, 2003) are compared specifically with MT III's from Can Llobateres and Piera in figures 6.35 and 6.36. These MT III's appear

similar in size with apparent increases in siM1 from Can Llobateres to Piera to *"Hippotherium" africanum*.

One MC III of *"Hippotherium" africanum* preserved M5, M1, and M3 and appears indistinguishable from the larger form from Can Llobateres on the basis of all three measurements (figs. 6.37 & 6.38). The favorable comparison between MC III's from Piera and the smaller form from Can Llobateres has already been noted.

If the Piera hipparion were to be considered a later and more derived form of *"Hippotherium" catalaunicum* (Bernor et al., 1989; Bernor et al., 1996b) represented by MC III's from Can Llobateres, then the nature of the morphological transition from *"Hippotherium" catalaunicum* to the Piera hipparion depends on which group of MC III's is assigned to *"Hippotherium" catalaunicum*. This transition would also be relevant to selection pressures on hipparion faunas across the Vallesian-Turolian boundary. Two morphological transitions appear possible: 1) a decrease in size and possible slight increase in relative metapodial breadth from the larger form with more slender MC III's (see arrow 1 in 6.37), or 2) a slight increase in relative MC III slenderness combined with stasis in terms of size (see arrow 2 in 6.37). The later possibility is marginally more parsimonious but further comparisons between the Piera and Can Llobateres hipparion samples not restricted to MP III's are necessary. The open nomenclature *"Hippotherium"* cf. *catalaunicum* (Can Llobateres) is adopted here to refer to the smaller form from Can Llobateres. *"Hippotherium"* aff. *catalaunicum* (Can Llobateres) is used for the larger form with a relatively more slender MC III diaphysis

The near identity in figures 6.37 and 6.38 of the single MC III of *"Hippotherium" africanum* and *"Hippotherium"* aff. *catalaunicum* (Can Llobateres) is notable and supports the idea of a *"Hippotherium" catalaunicum*-*"Hippotherium" africanum* clade in the Vallesian with a common biogeographic range (Bernor et al., 1996b). Again,

further study is needed but the morphological analyses of MP III's reported here are consistent with the hypothesis of a clade within the *Hippotherium primigenium* Complex with a circum-Mediterranean distribution (Bernor et al., 1996b).

A possible phylogenetic tree of such a circum-Mediterranean clade of the *Hippotherium primigenium* Complex is diagrammed in figure 6.39. The hypothesis shown is consistent with the review of Bernor et al. (1996b) and the results reported here relating to MP III morphology. Potential character-state transitions are shown with arrows and habitat scores are shown for each taxon.

If in fact two species are represented at Can Llobateres, it would appear that one was more likely to have exploited a more closed habitat niche while the second may have depended on some more open areas. The smaller species, *"Hippotherium"* cf. *catalaunicum* here, had clearly negative habitat scores suggesting a comparison with *Hippotherium primigenium* from Höwenegg a probable browser dependent on forested conditions (Kaiser, 2003). The larger species, *"Hippotherium"* aff. *catalaunicum,* appears likely to have exploited a possibly more open niche like that of *Hippotherium primigenium* from Eppelsheim which Kaiser (2003) argues included at least seasonally extended grassy areas.

Polinya

The single complete MC III from the MN 9 locality of Polinya in the Vallés-Penedés Basin appears intermediate between *"Hippotherium"* cf. *catalaunicum* (Can Llobateres) and *"Hippotherium"* aff. *catalaunicum* (Can Llobateres). It has habitat score of -0.14 which appears consistent with a paleoenvironment like that of Can Llobateres.

Can Ponsic

Like Can Llobateres, Can Ponsic (MN 9, Vallés-Penedés Basin) preserves specimens of *Dryopithecus* (Andrews et al., 1979) and may be slightly older than Can Llobateres (Agusti et al., 1997). The single partial MT III from Can Ponsic discussed here is consistent with *Hippotherium"* cf. *catalaunicum* (Can Llobateres). This specimen offers no evidence for a hipparion with a different paleohabitat than Can Llobateres.

La Tarumba and Villadecavalls vicinity

La Tarumba (Villadecavalls, Spain) in the Vallés-Penedés Basin has an MN 10 mammal correlation and is also known to preserve material of *Dryopithecus laietanus* like Can Llobateres. The habitat score for a single complete MC III from La Tarumba was -0.10 and on the basis of this score there is no reason to suggest differing conditions at La Tarumba compared to Can Llobateres, Can Ponsic, and Polinya. Sampling of complete MP III's is, however, poor and limits interpretation.

Piera

MP III's from the MN 11 locality of Piera in the Vallés-Penedés Basin have already been discussed in comparison to those from Can Llobateres and attributed to a single species, *"Hippotherium"* aff. *catalaunicum* (Piera) with a mean habitat score of -0.27 (N = 6) based on MC III's. This value is intermediate between that of the two forms from Can Llobateres and suggests a possible drop in hipparion diversity in the Vallés-Penedés Basin from the Vallesian to Turolian. A trend from two more specialized hipparions to a single possibly more generalized species would appear possible as two species with more extreme habitat scores are replaced with one species with a habitat score intermediate between those two. However, the negative habitat score for *"Hippotherium"* aff. *catalaunicum* (Piera) remains in sharp contrast with what appear to

be more open habitat forms from other areas in Spain like *Hipparion melendezi* from the Duero Basin and the hipparion from La Roma 2 in the Teruel area. While these species are likely older than *"Hippotherium"* aff. *catalaunicum* (Piera), hipparions from the MN 11 locality Puente Minero also in the Teruel area appear similar to those from La Roma 2 (Alcalá, 1994). Puente Minero also has a second much smaller species of hipparionine referred to *Hipparion gromovae* VILLALTA & CRUSAFONT 1957 (Alcalá, 1994). Thus, variability in likely hipparion habitat appears less extreme temporally from MN 9 to MN 11 in the Vallés-Penedés Basin than variability in hipparion habitat between regions such as that seen from Piera to Puente Minero.

Nombrevilla

Nombrevilla in the Daroca area of the Calatayud-Teruel Basin is the type locality for *"Hippotherium" koenigswaldi* SONDAAR 1961 which Bernor et al. (1996b) assign to the *Hippotherium primigenium* Complex. Nombrevilla is assigned to lower MN 9 (Morales et al., 1999) and predates other hipparion localities in the of the Calatayud-Teruel Basin The results here confirm MC III morphology like that of *Hippotherium primigenium* and different than that observed for the La Roma 2 MC III's. While no habitat scores could be calculated for *"Hippotherium" koenigswaldi*, it seems likely that they would be negative based on close similarity with the Höwenegg standard. *"Hippotherium" koenigswaldi* would most probably have been a forest-dweller.

La Roma 2

The site of La Roma 2 from the Teruel area of Calatayud-Teruel Basin is dated to MN 10 (Alcalá, 1994; Morales et al., 1999) and may be slightly younger than the MN 10 Valles-Penedes Basin sites in the vicinity of Villadecavalls. La Roma 2 is geographically

closer to the earliest Vallesian (upper MN 9) site of Nombrevilla in the Daroca area of the Calatayud-Teruel Basin (Morales et al., 1999).

The La Roma 2 hipparion specimens were referred to a single species *Hippotherium primigenium*. The morphological analysis of MP III's reported here is in clear agreement with the referral of the La Roma 2 specimens to a single species. The La Roma 2 MP III's clearly fall in single well-defined 95% confidence ellipses (figs. 6.2-6). The large sample and single species identity for the La Roma 2 hipparions was in part responsible for the use of the La Roma 2 sample as a comparative sample by Scott and Maga (in press) which has been followed here.

It is equally clear that the La Roma 2 hipparion is distinct from *Hippotherium primigenium* from Höwenegg. Compared to Höwenegg, the La Roma 2 MP III's are: 1) larger in terms of MGSV and M5 both (figs. 6.3-6), 2) relatively more slender as measured by siM3 (fig. 6.2), and 3) relatively longer as measured by siM1 (fig. 6.2). The relatively elongate and slender MP III's from La Roma 2 resulted in very positive habitat scores for the La Roma 2 hipparion (fig. 6.33; tab. 6.4) indicating a high probability of an open habitat preference.

There exists little evidence applicable to questions of higher level taxonomy for the La Roma 2 hipparion. Alcalá (1994) cites complex and plicated enamel in conjunction with large tooth size in favor of the *Hippotherium primigenium* attribution. Favorable comparison with *"Hippotherium" koenigswaldi* and *"Hipparion" truyolsi* were also made by Alcalá (1994). However, *"Hippotherium" koenigswaldi* and *"Hipparion" truyolsi* are clearly smaller than the La Roma 2 hipparion. Sondaar (Sondaar, 1961) reported ranges of MT III M10 for these species of 40.5 - 43.2 mm and 40.5 - 42.6 mm respectively for these species. These are ranges are both at the low end of the 39.77 - 49.19 mm MT III M10 range for the La Roma 2 hipparion. *"Hipparion"*

truyolsi also has an MN 13 type locality (Valdecebro II) and is likely much younger than the La Roma 2 hipparion. No recognized hipparionine species in the comparative sample of MP III's investigated here was comparable to the La Roma 2 hipparion in terms of size and relative elongation and slenderness of MP III's (tabs. 6.5 & 6.7). Thus, a conservative generic attribution and novel species attribution appears most appropriate for the La Roma 2 specimens and *"Hipparion"* sp. (La Roma) is proposed.

Alcalá (1994) applied the methodology of Andrews et al. (1979) to the La Roma 2 fossil assemblage. On the basis of a high percentage of large terrestrially quadrupedal species identified from La Roma 2 a more open environment appeared likely. Six of 16 species identified from La Roma 2 were identified as probable grazers (Alcalá, 1994). On this basis, Alcalá (1994) concluded in favor of a savanna/floodplain environment at La Roma 2.

The faunal list for La Roma 2 is reproduced in table 6.8 (Alcalá, 1994; Alcalá, 1997; NOW, n.d.) with dietary, locomotion and molar crown height categories as listed in the NOW mammal database (n.d.). The high habitat score for *"Hipparion"* sp. (La Roma) is consistent with an open habitat preference and grazing diet. This view is more consistent with Alcalá's (1994) reconstruction of La Roma 2 as a cool, dry savanna than with a possibly more wooded habitat suggested by the predominance of brachydont mixed feeders and browsers (per the NOW mammal database).

When compared to *"Hippotherium" koenigswaldi* from the earlier locality of Nombrevilla (MN 9) in the Calatayud-Teruel Basin, *"Hipparion"* sp. (La Roma 2) appears to signal a different probably drier and more open habitat. This could imply a paleoenvironmental shift across the MN 9/10 boundary in the Calatayud-Teruel Basin or a regional difference in habitats from Daroca to Teruel. In contrast, the MN 11 site of Puente Minero in the Teruel area appears to have a hipparion similar to that from La

Roma 2 in addition to the much smaller *Hipparion gromovae* (Alcalá, 1994). Less change in hipparion habitat preference appears likely from La Roma 2 to Puente Minero than from Nombrevilla to La Roma 2.

Concud

Concud is situated in the Teruel area of the Calatayud-Teruel Basin like La Roma 2 and Puente Minero but has a younger MN 12 mammal correlation (Alcalá, 1994; Morales et al., 1999). Collections assigned to Concud have some heterogeneity of provenience. Most specimens cataloged from Concud likely derive from the locality of Cerro de la Garita (Forsten, 1979; Alcalá, 1994). Sondaar (1961) defined Concud as inclusive of specimens from Cerro de la Garita and Barranco de las Calaveras and raised to specific rank *Hipparion concudense* from these localities. Forsten (1979) argued for a single species of hipparion without subspecific differentiation from Concud and the geographically and stratigraphically close sites of Masia del Barbo and Los Mansuetos. In contrast, Sondaar (1961) found that the hipparion sample from Los Mansuetos was likely a smaller form which was given the subspecific appellation *Hipparion concudense aguirrei* SONDAAR 1961. Thus, *Hipparion aguirrei* would be available for a smaller species of hipparion from Concud.

The results of analysis of MC III's and MT III's reported here indicated that the most variability within the Concud sample was in terms of relative MC III diaphysis breadth as measured by siM3 and seen in figures 6.2B and 6.5B. Consequently, two morphs were recognized from Concud: a broad morph and a slender morph. The two morphs from Concud parallel the situation at Can Llobateres where a species with relatively broader MC III's and a species with relatively more slender MC III's have been suggested. However, unlike the case with the two forms at Can Llobateres whose ranges for M5 abut each other and barely overlap, the two Concud morphs appear to overlap

broadly in terms of size. Moreover, the range given (Sondaar, 1961) for M5 of MC III's from Los Mansuetos (the type locality for *Hipparion concudense aguirrei*) overlaps much of the range for M5 of the Concud MC III's studied here. Without much better sampling, it is difficult to find a significant difference in size between the broad morph and slender morph from Concud. Thus, at this juncture, it appears best to follow Forsten (1979) and refer all the specimens from Concud to *Hipparion concudense*.

The mean habitat scores for *Hipparion concudense* of -0.29 (based on MC III's) and -0.59 (based on MT III's) suggest more closed habitats and are comparable to those of *"Hippotherium"* aff. *catalaunicum* (Piera) in the case of MC III's and *"Hippotherium"* cf. *catalaunicum* (Can Llobateres) in the case of MT III's. An alternative interpretation is suggested when habitat scores are summarized for the broad morph and slender morph individually. In this case, the broad morph has a very negative habitat score (-1.05) while the slender morph has a positive habitat score (0.28). Under this interpretation, more closed habitats would still be present but hipparions might also have utilized other more open habitats.

Alcalá (1994) concluded that Cerro de la Garita was likely a savanna - grouping Cerro de la Garita with La Roma 2 as opposed to La Gloria 4. However, based on an analysis of cenograms for a succession of Teruel localities from MN 10 to MN 14 (Alcalá, 1994), Cerro de la Garita appears to represent a peak in humidity and vegetation. Cerro del la Garita also contrasts with La Roma 2 in terms of the relative representation of grazers and browsers. Cerro del la Garita includes a higher proportion of browsers than La Roma 2 (Alcalá, 1994). Alcalá (1994) modeled habitats in terms of three dimensions of ecological diversity (dietary diversity, locomotor diversity, and diversity in body size) using the Shannon-Weaver index of diversity for each dimension. According to this model, the Cerro de la Garita fossil assemblage appears most like that of modern

woodland or bush country - heavy cover or light cover in the habitat classification of Kappelman et al. (1997) and Scott et al (1999). It would seem likely that Cerro de la Garita represents a more closed habitat than La Roma 2. The reconstruction of Cerro de la Garita as woodland or bush country is consistent with the habitat scores for *Hipparion concudense* from Concud (including Cerro de la Garita).

Los Mansuetos is stratigraphically and geographically close to Cerro de la Garita and has been reconstructed as more covered than Cerro de la Garita (Alcalá, 1994). If the broad morph of *Hipparion concudense* is the same as what Sondaar (1961) identifies as *Hipparion concudense aguirrei* then distinctions between Los Mansuetos and Cerro de la Garita (Alcalá, 1994) would argue for either a temporal or geographic succession of habitats in terms of cover. The broad and slender morphs of *Hipparion concudense* could be considered as tied to separate phases of this succession. Thus, variability in the Concud MP III's which apparently have somewhat heterogeneous provenience might be due to time averaging across a temporal succession of habitats. The broad and slender morphs could be considered time successive populations or species. Los Mansuetos could sample a more closed phase of this succession while Cerro de la Garita could sample a more open phase. Concud in general might sample multiple phases of such a succession.

La Gloria 4

The hipparion from La Gloria 4 has been referred to *Hipparion fissurae* CRUSAFONT & SONDAAR 1971 (Alberdi & Alcalá, 1992). However, Eisenmann and Mein (1996) found little similarity between the La Gloria 4 hipparion and material of *Hipparion fissurae* from Layna including the type specimen IPS 2104, an MT III. Instead, the La Gloria 4 hipparion was referred to *Hipparion* cf. *elegans* GROMOVA 1952 from Pavlodar, Kazakhstan (Eisenmann & Mein, 1996). The analysis reported here confirms the observations of Eisenmann and Mein (1996) that the La Gloria 4 MT III is

more slender than that of *Hipparion fissurae*. However, poor preservation combined with uncertain restoration of the Layna MT III has been advanced as a possible cause of differences between the Layna MT III and La Gloria 4 MT III (Alberdi & Alcalá, 1999).

Alberdi and Alcalá (1999) tabled measurements for two complete MC III's of one individual from Layna and several MC III's from other Spanish localities (La Gloria 4, La Calera, and Villalba Alta Río) which are referred to *Hipparion fissurae* and these measurements are plotted in figure 6.40. It is notable that the MC III's for the Layna individual are relatively broad compared to the other specimens. Moreover, the Layna individual plots outside the 95% confidence ellipse for the other MC III's. This is the same morphological contrast between La Gloria 4 and Layna observed first by Eisenmann and Mein (1996) and confirmed here. La Gloria 4, La Calera, and Villalba Alta Río are all in the Teruel area and have MN 14 mammal correlations while Layna is in Soria province and appears to belong to MN 15 (Alberdi & Alcalá, 1999). Thus, recognition of the contrasting diaphyseal morphology between Layna and La Gloria 4 has implications with regard to geographic and temporal trends.

While it is agreed that attributions should be made on the basis of morphology (Eisenmann & Mein, 1996), the significant biogeographic implications of the referral of a Spanish hipparion to a species of hipparion from Kazakhstan in this case require that attributions based on morphological similarity (even those designated "cf.") be supported by a very strong similarity based on a good sample of various elements. This does not appear to be the case here and the taxonomy for hipparions from Pavlodar and Kalmakpai appears complex in its own right (Forsten, 1997; Alberdi & Alcalá, 1999). The distinction between Layna and La Gloria 4 also appears legitimate (fig. 6.40). Thus, the more general attribution for the La Gloria 4 hipparion *Hipparion* aff. *fissurae* is preferred here.

The habitat score for the La Gloria 4 MT III is 1.27 which is at the extreme positive end of the habitat score spectrum and would suggest open environments. The same inference was made by Eisenmann and Mein (1996) based on this specimen and it was offered as evidence for a dry climate and open landscape. However, a fragmentary mandibular symphysis from La Gloria 4 appears to suggest a narrow muzzle typically associated with more selective feeders as opposed to grazers which might be expected in an arid, open habitat (Eisenmann & Mein, 1996).

La Gloria 4 is located in the Teruel area like La Roma 2 and Concud and has an MN 14 mammal correlation. Alcalá (1994) suggests that La Gloria 4 was drier, warmer, and more vegetated (based on cenograms) than earlier Teruel localities and concludes that La Gloria 4 was also more forested (in part based on analysis of ecological diversity). This result is intriguing in that it is consistent with both the slenderness of the La Gloria 4 MT III and the narrow mandibular symphysis from La Gloria 4. *Hipparion* aff. *fissurae* (La Gloria 4) could be reconstructed as a run-to-cover, cursorial, selective feeder inhabiting a dry, warm patchily forested habitat.

The abundance of taxa should have implications for paleoecology but most paleoecological analyses emphasize the presence or absence of taxa (e.g., Andrews et al., 1979). Alcalá (1994) noted that the La Gloria 4 *Hipparion* aff. *fissurae* (La Gloria 4) had a much lower relative representation than the La Roma 2 hipparion. Changes in relative abundance may result from changes in the absolute abundance of the taxonomic groups under consideration. For instance, if hipparion abundance is expressed relative to ruminant abundance an increase in hipparion relative abundance from one locality to another will result as long as hipparion numbers increase more or decrease less than ruminant numbers. Scott et al. (2003) proposed a simplifying model to convert within-locality relative abundance to between-locality absolute abundance. This model is applied

here with an assumption of constant ruminant plus hipparion biomass to data presented by Alcalá (1994) for Teruel localities and to published data for Los Valles de Fuentidueña (Alberdi, 1981; Morales & Soria, 1981) and the results are shown in figure 6.41. For the Teruel sequence, this model suggests that a hipparion dominated fauna persisted from MN 10 to MN 13 with a sharp drop in hipparion density and a concomitant rise in ruminant density in MN 14 as represented by La Gloria 4. Thus, the place of *Hipparion* aff. *fissurae* (La Gloria 4) in the La Gloria 4 fauna would appear different than that of hipparions in earlier faunas.

The possibility that emerges from a review of the totality of evidence available for La Gloria 4 is that as a result of environmental change (possibly an increase in aridity) hipparions became a less dominant component of the fauna and specialized in a specific niche (run-to-cover, selective feeder) supporting a lower density population. While the overall environment at La Gloria 4 may have been more closed than at earlier localities (Alcalá, 1994), *Hipparion* aff. *fissurae* could have exploited a niche dependent on selective feeding and open patches. Reduced hipparion density could be the result of a shift towards specialization on specific habitat type as earlier habitats disappear.

El Firal

Little can be said regarding hipparions from the lower MN 9 *Dryopithecus fontani* locality of El Firal in the Seu d'Urgell Basin of the Pyrenees as no complete specimens appear to be preserved. Previously, Truyols (1958) referred to hipparions from El Firal as *Hipparion* sp. and Alberdi (1974) referred them to *Hippotherium primigenium*. The M5 measurements for three fragmentary MC III's suggest a hipparion that is on average smaller than *Hippotherium primigenium* from Höwenegg.

Ballestar

Like El Firal, Ballestar is in the Seu d'Urgell Basin and on the basis of size the Ballestar hipparion could be conspecific with that from El Firal. As already noted it was not possible to distinguish the single well-preserved, complete MP III (the MT III BA019) from either *Hippotherium primigenium* or *"Hippotherium"* cf. *catalaunicum* (Can Llobateres). The habitat score for BA019 was intermediate (=0.10; inside the Höwenegg range but outside the 95% confidence interval for the mean). *Hippotherium primigenium* from Eppelsheim is poorly sampled but appears to have had higher habitat scores than those for *Hippotherium primigenium* from Höwenegg (tab. 6.4). Kaiser (2003) suggests that at Eppelsheim *Hippotherium primigenium* utilized grassy areas such as reed flats at least seasonally. A similar habitat preference would be compatible with the habitat score for the Ballestar hipparion.

Venta del Moro

The three MP III's from the MN 13 locality of Venta del Moro describe a small hipparion with elongate and slender metapodials and a positive habitat score suggesting preference for open habitats.

Layna

As has been noted in the discussion of La Gloria 4, the type specimen of *Hipparion fissurae* from the MN 15 locality of Layna (Soria, Spain) is a very elongate MT III, but has a markedly high value for siM3 indicating a relatively broad diaphysis leading to a low habitat score of -0.36. MC III measurement for an individual from Layna also suggests a relatively broad MP III diaphysis (fig. 6.40) for *Hipparion fissurae* s.s. If MP III slenderness is related to aridity (Eisenmann, 1995; Eisenmann & Mein, 1996), then Layna may represent a more humid environment than La Gloria 4.

Fossil hipparionines from Greece

Pikermi

The two groups distinguished from Pikermi likely correspond to *"Hippotherium" brachypus* and *Cremohipparion mediterraneum*. Scores for siM1 and siM3 were computed for mean measurements reported for these two species (Koufos, 1987) and are shown in figure 6.8. The MP III's plotted here in figure 6.8 correspond reasonably with these mean based values for *"Hippotherium" brachypus* and *Cremohipparion mediterraneum*. Accordingly, small and elongate MP III's from Pikermi are assigned to *Cremohipparion mediterraneum* while larger but relatively shorter and broader MP III's are assigned to *"Hippotherium" brachypus*.

"Hippotherium" brachypus appears to be similar in size or perhaps slightly larger than *Hippotherium primigenium* from Höwenegg and appears to have MP III's with generally similar morphology. The mean habitat scores computed based on MC III's and MT III's were -0.53 and -0.57 respectively and would suggest a habitat preference for more closed settings similar to that of *Hippotherium primigenium* from Höwenegg.

Cremohipparion mediterraneum is smaller in size than *Hippotherium primigenium* from Höwenegg and displays a contrasting morphology or relative MP III elongation. The positive mean habitat scores for *Cremohipparion mediterraneum* suggest habitat preferences for more open environments which is consistent with evidence for a mixed diet of graze and browse for *Cremohipparion mediterraneum* (Hayek et al., 1992).

Cremohipparion mediterraneum has commonly been used as an analytic standard in studies of hipparion metapodial morphometry. The sample of MP III's from Pikermi attributed to *Cremohipparion mediterraneum* may serve as a good analytic standard representative of a hipparion that preferred habitats with more open areas. One possible problem with the use of *Cremohipparion mediterraneum* as a standard in future analyses

has to do with the possibility that *Cremohipparion mediterraneum* MP III's may be confused with those of *Hipparion prostylum* GERVAIS 1849 (Bernor et al., 1996b).

Hipparion prostylum has been recognized from Pikermi based on complete skull (BMNH M42603) (Woodburne & Bernor, 1980; Bernor et al., 1989; Bernor et al., 1996b). However, it has not been possible to identify this species on the basis of MP III's at Pikermi. Plots of PC1 versus MGSV and siM3 versus siM1 for *Cremohipparion mediterraneum* and *"Hippotherium" brachypus* from Pikermi and *Hipparion prostylum* from Mont Luberon (the type locality for *Hipparion prostylum*) demonstrate the difficulty of distinguishing between the similarly proportioned MP III's of *Cremohipparion mediterraneum* and *Hipparion prostylum* (see especially figs. 6.19A & 6.20A).

Two other species of hipparion have been listed from Pikermi: *Hipparion gettyi* BERNOR 1985 and *Cremohipparion* aff. *matthewi* (Bernor et al., 1996c). The small size of *Cremohipparion* aff. *matthewi* should make it readily identifiable at Pikermi and if it is present it may well be rare. MP III's for *Hipparion gettyi* have not yet been identified and described.

Samos

Based on size and morphology, MP III's from Samos have been assigned to seven different Morphs. Each of these could correspond to a separate species and various workers have recognized that the fossiliferous beds at Samos likely sample multiple species (Sondaar, 1971; Forsten, 1980; Bernor et al., 1996b; Bernor et al., 1996c). Sondaar (1971) suggested the possibility of five species at Samos with three of them being formally named species: *Cremohipparion matthewi* ABEL 1926, *Cremohipparion proboscideum* STUDER 1911, and *Hipparion dietrichi* WEHRLI 1941. Forsten (1980) was more emphatic in arguing for a total of five species at Samos including an unnamed

middle sized species and an unnamed large species. According to Forsten (1980) as many as four of these species are recorded at one locality (= Quarry 4). Of the seven MP III Morphs discussed here, five of them included multiple well-preserved specimens. Thus, the results of this study are broadly congruent in terms of species number with prior works focusing on Samos comprehensively.

Other additional hipparionine species have also been suggested for Samos. The skull AMNH 20628 referred by Forsten (1980) to an unnamed middle-sized hipparion was recognized as referable to *"Hippotherium" giganteum* GROMOVA 1952 from Grebeniki in the Ukraine (Woodburne & Bernor, 1980). *Cremohipparion nikosi* BERNOR & TOBIEN 1989 is based on a cranial fragment of unknown stratigraphic provenience and is thought to be similar to *Cremohipparion matthewi* in size and morphology with a more retracted nasal incision (Bernor & Tobien, 1989). Bernor et al. (1996b) reports that material of *Hipparion gettyi* BERNOR 1985 and *Hipparion prostylum* GERVAIS 1849 from Samos can be found in the collections of the Hungarian Geological Survey. Several named species appear possible for the Samos beds but matching the various species reported for Samos based on cranial material with MP III's is an uncertain task given the lack of associated crania and postcrania (Sondaar, 1971).

Quarry 5 is the youngest of the Samos localities considered here. It is thought to be best correlated with the top of MN 12 or very base of MN 13 and is constrained paleomagnetically to between 6.7 and 7 Ma (2003). MP III's from Quarry 5 were assigned to three different Morphs here: Samos Dwarf Elongate Morph, Samos Small Elongate Morph, and Samos Midsize Elongate Morph.

A consensus that *Cremohipparion matthewi* is restricted to Quarry 5 (Sondaar, 1971; Forsten, 1980) combined with a clear indication of smaller size suggests that the smallest MP III's from Quarry 5 probably belong to *Cremohipparion matthewi*. The five

small MC III's shown in figures 6.11 and 6.12 are numbered AMNH 23054 and four of these are photographed in Sondaar (1971) and referred to *Cremohipparion matthewi*. Two of those shown in Sondaar (1971)appear more robust and likely correspond to the two specimens that plot near AMNH FM140292 from Quarry 6 in terms of M1, M3, and M5 (see figs. 6.11 & 6.12). The other three specimens are placed in the Samos Dwarf Elongate Morph with four well-preserved MT III's also from Quarry 5. It appears likely that the Samos Dwarf Elongate Morph is best referred to *Cremohipparion matthewi*. Another unnamed species may correspond to the Samos Small Shortened Morph as represented by the MC III AMNH FM140292 from Quarry 6 and possibly two other MC III's from Quarry 5 (see figs. 6.11 & 6.12). On the basis of size, *Cremohipparion nikosi* could also be a possible candidate for association with the Samos Small Shortened Morph. Sexual dimorphism is also a possibility and the Samos Small Shortened Morph could in theory represent males of *Cremohipparion matthewi*. The firm association between the Samos Dwarf Elongate Morph and *Cremohipparion matthewi* is preferred here. Based on this interpretation, *Cremohipparion matthewi* has an intermediate habitat score of 0.15 based on MT III's. This is consistent with a grazing diet inferred for *Cremohipparion matthewi* (Hayek et al., 1992). However, the habitat score is not extreme and likely indicates the presence of some significant cover. The small size of *Cremohipparion matthewi* makes crypsis in areas of cover more possible. The elongate metapodials of *Cremohipparion matthewi* may be a sign of run-to-cover predator avoidance behavior. *Cremohipparion matthewi* may have grazed in open areas and retreated rapidly to areas of cover to avoid predation.

In addition to *Cremohipparion matthewi*, Sondaar (1971) suggested that a second larger species of hipparionine was represented at Quarry 5. This form is described as middle-sized and gracile by Forsten (1980) who also suggested a third even larger species

was present at Quarry 5. The results of this analysis split the MC III's referred to *Hipparion* sp. by Sondaar (1971) between two Morphs: the Samos Small Elongate Morph, and the Samos Midsize Elongate Morph. Among the specimens reviewed here, there is no evidence of Forsten's (1980) larger species unless it is the Samos Midsize Elongate Morph. A conservative approach would be to retain MC III's not assigned to *Cremohipparion matthewi* from Quarry 5 in a single species (= *Hipparion* sp. SONDAAR 1971) following Sondaar (1971). The mean habitat score for this species based on MC III's would be -0.12. This would suggest a second species of hipparion at Quarry 5 with a habitat preference for more covered areas than *Cremohipparion matthewi*. It is important to note, however, that the Samos Small Elongate Morph MC III's from Quarry 5 have positive habitat scores of 0.27 and 0.11. A single MT III from Quarry 5 was assigned to the Small Elongate Morph and had a habitat score of -0.22. These scores are neither extremely negative nor extremely positive and are suggestive of intermediate habitat preferences.

Without a larger sample of MP III's from Quarry 5 at Samos it is difficult to draw many conclusions. However, it would appear that at least two hipparionine species are present and that habitat preferences were neither for extremely forested nor extremely open habitats. Two MC III's from Quarry 5 shown in figures 6.11 and 6.12 are assigned to the Samos Small Shortened Morph and could be conspecific with the single MC III from the older Quarry 6. If this is the case then three species would be present at Quarry 5.

Quarry 6 is the oldest of the Samos localities with a likely mammal correlation of MN 11 and absolute age constrained between 7.8 and 8 Ma (Kostopoulos et al., 2003). A single MC III from Quarry 6 was available for study and it is assigned to a Samos Small Shortened Morph. This specimen had a habitat score of -0.90 which is comparable to the

mean habitat score for *Hippotherium primigenium* from Höwenegg. Without more specimens from Quarry 6, few conclusions can be drawn. However, this specimen suggests closed habitat conditions at Samos at ca. 7.9 Ma.

Quarry 4 and Quarry 1 are intermediate in age between Quarry 5 and Quarry 6 (Kostopoulos et al., 2003). The biostratigraphic horizon for Quarry 4 is constrained to between 7.45 Ma and 7.65 Ma and Quarry 1 is constrained to between 7.1 and 7.2 Ma (Kostopoulos et al., 2003). Quarry 1 may be the most diverse of the Samos localities in terms of hipparionines with as many as four possible species (Forsten, 1980). Sondaar was more conservative (1971) recognized two species each from Quarry 1 and Quarry 4: *Hipparion dietrichi* and *Cremohipparion proboscideum* from Quarry 1, and *Hipparion dietrichi* and a large species from Quarry 4.

According to this analysis, Quarry 1 had specimens assigned to four morphs and Quarry 4 had specimens assigned to three morphs (tab. 6.6). Both Quarry 4 and Quarry 1 had specimens assigned to the Samos Large Morph. These larger MP III's had a morphology intermediate between the Höwenegg and La Roma 2 standards in terms of elongation and slenderness (fig. 6.10). Among larger skulls from Quarry 1 and Quarry 4 there appears to be evidence for greater species diversity. The type of *Cremohipparion proboscideum* has a double POF (presumably preorbital plus caninus fossa) situated close to the orbit while large skulls from Quarry 1 and Quarry 4 have a POF situated farther from the orbit. Thus, two large hipparions may be represented at Samos: one with a double POF near the orbit and one with a single POF farther from the orbit. Associating the larger MP III's from Samos with these to skull forms is not possible without associated limb bones and skulls. Moreover, the larger MP III's from Samos do not appear to be divisible on grounds of morphology. Thus, the Samos Large Morph is referred here to *Cremohipparion* cf. *proboscideum*. The negative mean habitat scores

based on MT III's and MC III's assigned to the Samos Large Morph (=*Cremohipparion* cf. *proboscideum*) suggest the presence of habitat cover. This is consistent with reconstruction of *Cremohipparion proboscideum* as a mixed feeder on the basis of dental microwear (Hayek et al., 1992).

According to Sondaar (1971) the remaining hipparionines from Quarry 4 and Quarry 1 would be assigned to *Hipparion dietrichi*. This would include metapodials assigned to the Small Elongate Morph, the Small Slender Morph, and the Midsize Elongate Morph. It seems likely that these metapodials can be assigned to a minimum of two species: *Hipparion dietrichi* and *"Hippotherium" giganteum*. Forsten (1980) grouped a few postcrania from Quarry 1 with "…middle sized skulls of with an oval, triangular, double preorbital fossa situated as a mean 2.9 cm from the eye." One of these skulls, AMNH 20628, was referred to *"Hippotherium" giganteum* (Woodburne & Bernor, 1980). Thus, some of the MP III's from Quarry 1 could belong to *"Hippotherium" giganteum*. Other skulls from Quarry 1 include the larger ones that probably could be associated with the *Cremohipparion* cf. *proboscideum* MP III's and some moderate sized skulls similar to the type of *Hipparion dietrichi*.

An MC III, AMNH 23046, from Quarry 1 has been attributed to *Hipparion* cf. *dietrichi* (Sondaar, 1971). Here, it is grouped in the Small Elongate Morph. Small Elongate Morph and Midsize Elongate Morph specimens from Quarry 5 have been conservatively referred to *Hipparion* sp. SONDAAR 1971 here. Thus, AMNH 23046 could also belong to *Hipparion* sp. SONDAAR 1971. If this were the case, then the two remaining MP III Morphs from Quarry 1 (= Samos Small Slender Morph and Samos Midsize Elongate Morph) would be candidates for *Hipparion dietrichi* and *"Hippotherium" giganteum*. However, an alternative solution is preferred here.

Sondaar (1971) noted the possibility that *Hipparion* sp. SONDAAR 1971 was a variety of *Hipparion dietrichi*. Thus, as an alternative to recognizing *Hipparion* sp. SONDAAR and *Hipparion dietrichi* at Quarry 1, it is proposed that MC III AMNH 23046 from Quarry 1 assigned to the Small Elongate Morph and the MT III AMNH 23043E from Quarry 1 assigned to the Midsize Elongate Morph be referred provisionally to *Hipparion* cf. *dietrichi*. The combining of Small Elongate Morph and Midsize Elongate Morph specimens into a single species is the same solution as that used for the Samos Small Elongate and Midsize Elongate MP III's from Quarry 5. This assignment is consistent with a hipparionine lineage with elongate MP III's and moderate size composed of *Hipparion* cf. *dietrichi* at Quarry 1 and *Hipparion* sp. SONDAAR at Quarry 5 and is the possibility that these two forms may belong to a single chronospecies.

Once the Samos Small Elongate Morph and Samos Midsize Elongate Morph at Quarry 1 are assigned to *Hipparion* cf. *dietrichi* and the Samos Large Morph at Quarry 1 is assigned to *Cremohipparion* cf. *proboscideum*, then the Samos Small Slender Morph is left as a possible candidate for MP III's assignable *"Hippotherium" giganteum* known from AMNH 20628 at Quarry 1 (Woodburne & Bernor, 1980). Thus, very provisional assignment of Samos Small Slender Morph MP III's to *"Hippotherium"* aff. *giganteum* is suggested.

The linkages between species and Morph made for Quarry 1 were also applied to Quarry 4. This resulted in assigning Samos Small Slender specimens from Quarry 4 to *"Hippotherium"* aff. *giganteum*, Samos Midsize Elongate specimens from Quarry 4 to *Hipparion* cf. *dietrichi*, and Samos Large Morph specimens from Quarry 4 to *Cremohipparion* cf. *proboscideum*. The same associations between provisional species identification and MP III Morph were made for specimens where exact provenience was

uncertain. A complete accounting of MP III's from Samos by Quarry, Morph, and provisional species identification is shown in table 6.6.

Mean habitat scores were calculated based on all specimens assigned to *Hippotherium"* aff. *giganteum* and *Hipparion* cf. *dietrichi*. In the case of *Hippotherium* aff. *giganteum*, these scores were the same as that reported already for the Small Slender Morph (= 1.62 based on four MT III's). *Hipparion* cf. *dietrichi* resulted in mean habitat scores of -0.11 based on MC III's and 0.04 based on MT III's. According to these scores and those for *Cremohipparion* cf. *proboscideum*, it would appear that hipparions known from Quarry 1 and Quarry 5 of Samos (MN 12 mammal correlation) had a wide range of habitat preferences and options from open and dry zones (probable for *Hippotherium"* aff. *giganteum* with its slender MT III's) to areas of cover suitable for a mixed feeder (e.g., *Cremohipparion* cf. *proboscideum*). The association between the Samos Small Slender Morph MT III's and "*Hippotherium" giganteum* skulls is still uncertain. However, the very positive habitat score for the Samos Small Slender Morph would be most consistent with a grazing diet. Studies of dental mesowear and microwear on material of "*Hippotherium" giganteum* may clarify this issue; although the preliminary work of is that Hayek et al. (Hayek et al., 1992) suggested a browsing diet for "*Hippotherium" giganteum*.

What is most evident is great complexity of the situation with respect to hipparions from Samos. Clearly multiple species of differing sizes and contrasting MP III morphology are present at the Samos localities discussed here. Despite a sample of 19 MT III's and 14 MC III's available for study here, the samples at each individual Quarry are not really adequate given the hipparion diversity apparent at Samos in general. Understanding the Samos hipparions is further complicated by absence of cases of associated crania and postcrania.

Ravin de la Pluie

Ouranopithecus is known from Ravin de la Pluie (Axios Valley, Greece) which has a Vallesian MN 10 mammal correlation. Three hipparionine MT III's from Ravin de la Pluie were analyzed here. These specimens were placed in three separate species by Koufos (2000b) and all three species were considered as inhabitants of a "savannah-like province" following de Bonis et al. (1992).

The results presented here for these three MT III's support the conclusion in favor of at least two and possibly three separate hipparion species at Ravin de la Pluie. RPl-38 referred to *Cremohipparion macedonicum* by Koufos (2000b) is clearly smaller in size, more slender, and more elongate than RPl-61 and RPl-39. RPl-61 is smaller than RPl-39 but similar in shape: both specimens plot within the Höwenegg 95% confidence ellipse for siM3 versus siM1. Here, the problem of sampling impacts the conclusion regarding whether these specimens represent one or two species. RPl-61 clearly comes from a hipparion smaller than *Hippotherium primigenium* from Höwenegg but RPl-39 is in the lower end of the size range for the Höwenegg sample and thus it is conceivable that the two specimens sample the opposite size extremes of a hipparion on average smaller than *Hippotherium primigenium* from Höwenegg. Deference is given here to the conclusions of Koufos (2000b) which are based on a consideration of other elements and comparison with the Pentalophos 1 sample of *Hipparion* aff. *depereti* which compares in terms of size to RPl-61. Thus, RPl-61 is referred to *Hipparion* aff. *depereti*, RPl-39 is referred to *Hippotherium primigenium*, and RPl-38 is referred to *Cremohipparion macedonicum*.

The habitat scores generated for these three species are thus based only on a single specimen each but vary widely. A habitat score of 1.32 for *Cremohipparion macedonicum* is a clear indicator of a habitat preference for open areas and is not inconsistent with the conclusions of de Bonis (de Bonis et al., 1992). However, the other

two species from Ravin de la Pluie would appear to have had different habitat preferences. Habitat scores of -0.31 for *Hippotherium primigenium* and 0.06 for *Hipparion* aff. *depereti* are intermediate between the La Roma 2 and Höwenegg standards and would imply intermediate habitats with some cover.

Saloniki

Cremohipparion matthewi, *Hipparion dietrichi*, *Cremohipparion* cf. *mediterraneum*, and a fourth larger species of hipparionine have all been reported for Saloniki (Zouhri & Ben Moussa, 2000) and assigned a Turolian age. Therefore, the Saloniki specimens are plotted in figure 6.42 in conjunction with specimens of *Cremohipparion matthewi* from Samos, *Hipparion* cf. *dietrichi* from Samos and Akkaşdağı, and *Cremohipparion mediterraneum* from Pikermi. MNHNSLQ667 was assigned to *Cremohipparion matthewi* by Zouhri and Ben Moussa (2000) and compares favorably with MT III's from Samos assigned to *Cremohipparion matthewi*. However, the MT III, MNHNSLQ663, and the MC III, MNHNSLQ487, which are attributed to *Hipparion dietrichi* by Zouhri and Ben Moussa (2000) appear small and have higher scores for PC1 than the specimens of *Hipparion* cf. *dietrichi* from Samos and Akkaşdağı. These specimens potentially compare better with *Cremohipparion mediterraneum* from Pikermi while MNHNSLQ652 which was assigned by Zouhri and Ben Moussa (2000) to *Cremohipparion* cf. *mediterraneum* is comparable to both *Hipparion* cf. *dietrichi* from Samos and *Cremohipparion mediterraneum* from Pikermi. It is possible that the MT III's from Saloniki studied here fall into three species as concluded by Zouhri and Ben Moussa (2000) but the variability in these specimens could be also subsumed in a single species or split between *Cremohipparion matthewi* and a second species including specimens assigned by Zouhri and Ben Moussa (2000) to *Cremohipparion* cf. *mediterraneum* and *Hipparion dietrichi*.

Zouhri and Ben Moussa (2000) assigned the MC III, MNHNSLQ490, to a separate larger unnamed species. This is supported here and MNHNSLQ490 is particularly notable for its low habitat score of -0.54. This suggests the presence of at least an intermediate habitat characterized by some cover. Exact provenience is unknown for this specimen.

All other specimens analyzed here other than MNHNSLQ490 are notable for positive habitat scores (tab. 6.4) and regardless of species level sorting indicate one or more species of hipparion with preferences for more open and probably drier habitats.

Maramena

The two MT III's analyzed here from Maramena appear to compare well with *Cremohipparion matthewi* from Samos and are assigned to *Cremohipparion* cf. *matthewi*. The habitat scores for these two specimens (0.32 and 0.38) are consistent with the habitat reconstruction for *Cremohipparion matthewi* from Samos of grazing in open areas with possible retreat to some areas of cover.

Fossil hipparionines of Central Europe

Höwenegg

The Höwenegg (Hegau, Germany) hipparion has been referred by Bernor et al. (1996b) to *Hippotherium primigenium* STAGE-OF-EVOLUTION III distinguishing it at the population level from material from the *Hippotherium primigenium* type locality of Eppelsheim. The sample of MP III's from Höwenegg can be distinguished from the single complete MT III and single complete MC III from Eppelsheim which are both relatively more slender. However, this difference is likely a population level one and the totality of the evidence from the Höwenegg skeletons supports its assignment to *Hippotherium primigenium* (Bernor et al., 1997). *Hippotherium primigenium* from

Höwenegg is treated here as a single population standard for comparison and the sizes of the Höwenegg 95% confidence ellipses for siM3 versus siM1 and PC1 versus MGSV compares with those from La Roma 2 where a single species of hipparion also appears likely. *Hippotherium primigenium* from Höwenegg is considered a browsing inhabitant of subtropical mesophytic forest (Bernor et al., 1988; Bernor et al., 1997; Kaiser, 2003) and had mean habitat scores of -0.99 for MC III's and -0.74 for MT III's. This supports the hypothesis that forest-dwelling hipparions tend to have broader and shorter MP III's like forest dwelling bovids and that more negative habitat scores can be linked to more closed habitats among bovids and hipparions.

Höwenegg has been dated radiometrically to 10.3 Ma (Swisher, 1996). Thus, Höwenegg provides a MN 9 example of what appears to have been a forested environment from which no hominoids are currently known.

Eppelsheim

The two Eppelsheim MP III's of *Hippotherium primigenium* are relatively more slender than those of *Hippotherium primigenium* from Höwenegg but were otherwise similar. As a consequence of their greater slenderness, these specimens resulted in positive habitat scores of 0.09 and 0.87 suggesting preferences for more open areas. This is in agreement with the conclusion of Kaiser (2003) based on dental mesowear in favor of habitats with seasonally extended grassy areas for *Hippotherium primigenium* from Eppelsheim.

Eppelsheim is part of the 'Dinotheriumsande' deposits (Mainz, Germany), has an MN 9 mammal correlation (Franzen & Storch, 1999), and is geographically not distant from Höwenegg. Thus, *Hippotherium primigenium* from Eppelsheim would appear to be a population of *Hippotherium primigenium* not far removed temporally and

geographically from the Höwenegg population of *Hippotherium primigenium*. These two populations would, however, appear to have had different habitat preferences.

Esselborn

The two MT III's from Esselborn (another MN 9 'Dinotheriumsande' locality) studied here appear to be much like those of *Hippotherium primigenium* from Höwenegg and are referred to *Hippotherium primigenium*. These two specimens had negative habitat scores suggesting that they were tied to habitats more like those of the *Hippotherium primigenium* from Höwenegg than those of *Hippotherium primigenium* from Eppelsheim.

Dorn-Dürkheim

Dorn-Dürkheim 1 (Mainz, Germany) is in the same immediate vicinity as Eppelsheim and Esselborn but has a younger Turolian age (= MN 11) (Franzen & Storch, 1999). The hipparions from Dorn-Dürkheim have recently been discussed in some depth (Kaiser et al., 2003) and two species are recognized from Dorn-Dürkheim: *Hippotherium primigenium* and *Hippotherium kammerschmitti*.

Hippotherium kammerschmitti is the smaller of the two species and would appear to also be the more cursorial of the two as well as more dedicated to a diet of browse (Kaiser et al., 2003). *Hippotherium primigenium* from Dorn-Dürkheim was reconstructed as a less cursorial, mixed feeder (Kaiser et al., 2003). The habitat score for the type specimen of *Hippotherium kammerschmitti* (the MC III SMF-DD4435) was -0.07 which is above that of the two complete MT III's from Dorn-Dürkheim assigned to *Hippotherium primigenium*. Thus, the habitat scores of the Dorn-Dürkheim hipparions are consistent with environments that include significant browse. Franzen and Storch (1999) argued for an environment of diverse woodland areas at Dorn-Dürkheim and this analysis is consistent with that interpretation.

Charmoille

The fauna of Charmoille (Ajoie, Switzerland) in the 'Vogesensande' is not well-studied but is thought to be an MN 9 locality (Franzen & Storch, 1999). The hipparion from Charmoille would appear to be a smaller bodied variant of the similarly aged *Hippotherium primigenium* from Höwenegg. Study of a larger sample of specimens from Charmoille might make clear a substantive difference in size worthy of designation as a separate species. It would seem equally likely that the Charmoille hipparion is simply another population of *Hippotherium primigenium*. Here, the Charmoille hipparion is referred to *Hippotherium* cf. *primigenium* pending further study. The habitat scores for the Charmoille MP III's are on the whole very negative and suggest a habitat preference similar to that of *Hippotherium primigenium* from Höwenegg.

Rudabánya

The Rudabánya hipparions have been discussed recently and two species were considered likely (Bernor et al., 2003a). The larger of these is *Hippotherium intrans* which was reconstructed as a mixed feeder with elongate MT III's. While the type of *Hippotherium intrans* is clearly relatively elongate, it is also not slender and resulted in an estimated habitat score of -1.36. This suggests both a wet environment and one that also selected for cursorial locomotion. This is consistent with mixed-feeder dietary signal for *Hippotherium intrans* and the previous conclusion (Bernor et al., 1988; Bernor et al., 2003a) in favor of equable subtropical forest environments near the Pannonian lake side with more open country mesophytic woodlands more distal to the lake. The smaller form from Rudabánya resulted in similarly negative habitat scores and were also elongate but broad. The smaller Rudabánya form appears similar to an MC III from Gols is provisionally referred to the same species – "*Hipparion*" sp. 2 (Vienna Basin) (see below).

Inzersdorf

Inzersdorf in the Vienna Basin is assigned to MN 9 possibly slightly older than Höwenegg (Steininger et al., 1996). A single species of hipparion smaller than *Hippotherium primigenium* from Höwenegg appears likely at Inzersdorf. This hipparion compares favorably to both the Baltavár hipparion and *Hippotherium primigenium* from Höwenegg in terms of relative elongation and could be related to one or both of these. The Inzersdorf hipparion is referred here to "*Hipparion*" sp. 1 (Vienna Basin) pending further study. The negative mean habitat scores for "*Hipparion*" sp. 1 (Vienna Basin) suggest a preference for forested environments.

Prottes

Like Inzersdorf, Prottes is in the Vienna Basin and a single MT III from Prottes compared fairly closely with the Inzersdorf MT III's in terms of size, relative elongation and relative slenderness. The Prottes MT III (NHMW9101) is provisionally referred to "*Hipparion*" sp. 1 (Vienna Basin). A sample of one is a poor basis for a habitat inference but the habitat score of -0.06 for the Prottes MT III would be consistent with closed or intermediate environments.

Gols

The two MC III's from the Vienna Basin locality of Gols appear to represent two different species. Both specimens differ from the Inzersdorf hipparion: NHMW1383/3 appears to be larger and NHMW1383/1 appears relatively more elongate. The smaller, elongate but broad MC III, NHMW1383/1, would appear to compare favorably with the small form from Rudabánya. Provisionally, the small form from Rudabánya and the small elongate Gols MC III are referred to "*Hipparion*" sp. 2 (Vienna Basin). The habitat score for NHMW1383/1 was -0.65 and is consistent with mainly forested habitats.

The other Gols MC III, NHMW1383/3, is larger, relatively more slender, and relatively short. This specimen is provisionally placed in a third Vienna Basin species, "*Hipparion*" sp. 3 (Vienna Basin). NHMW1383/3 had a positive habitat score of 0.49 possibly signaling a greater reliance on more open mesophytic woodlands.

The situation at Gols may in some way parallel that at Rudabánya with the presence of two species potentially ranging between more densely covered areas and more open woodlands. These habitats might vary in their distance from water.

Schwechat

The single MC III from Schwechat in the Vienna Basin compares favorably with the Inzersdorf MC III's and is provisionally referred here to the same species, "*Hipparion*" sp. 1 (Vienna Basin). The habitat score for this specimen was -0.28 which is consistent with a preference forested habitats for "*Hipparion*" sp. 1 (Vienna Basin).

Sümeg

Sümeg which is near Lake Balaton in Hungary has been correlated with MN 10 (Kordos, 1992) and would thus appear to be intermediate in age between Rudabánya and Csákvár. The type specimen for *Hippotherium sumegense*, MAFIV13242, from Sümeg (Hungary) has been discussed recently (Bernor et al., 1999) and was included in this study. It resulted in a very negative habitat score of -1.31 which is consistent with the previous interpretation of *Hippotherium sumegense* as a forest living hipparion.

Csákvár

The hipparions from Csákvár correlated to MN 11 (Kordos, 1992) were divided into the Csákvár Elongate Morph and the Csákvár Shortened Morph. The Csákvár Elongate Morph MT III's appear to compare closely with the type of *Hippotherium intrans* from Rudabánya (6.15A) and therefore the Csákvár Elongate Morph is identified

as *Hippotherium* cf. *intrans* here. The MC III of the Csákvár Elongate Morph thus assigned to *Hippotherium* cf. *intrans* yielded a habitat score of -0.65. This is not inconsistent with the habitat interpretation for *Hippotherium intrans* at Rudabánya in favor of open mesophytic woodlands to subtropical forests.

The Csákvár Shortened Morph compares closely with *Hippotherium primigenium* from Höwenegg, *Hippotherium brachypus* from Pikermi, and *"Hippotherium"* cf. *brachypus* from Akkaşdağı (figs. 6.15A, 6.16A, & 6.43). Given the MN 11 age of the Csákvár assemblage, the Csákvár Shortened Morph is attributed to *"Hippotherium"* cf. *brachypus* here. The mean habitat score of 0.14 (based on two MC III's) suggests the use of some intermediate environments while the mean habitat score of -0.40 (based on two MT III's) is more consistent with the inference of a closed habitat preference for *Hippotherium brachypus*.

Polgárdi

The Polgárdi MP III's appear similar to those of *"Hippotherium"* cf. *brachypus* from Csákvár (=Csákvár Shortened Morph) (figs. 6.15A, 6.16A, 6.17, & 6.43). Thus, on the basis of MP III morphology and pending further study, the Polgárdi specimens are considered *"Hippotherium"* cf. *brachypus* here. The Polgárdi specimens differ from those from Csákvár mainly by being slightly more slender. This translates into higher habitat scores (0.10 based on MC III's and 0.04 based on MT III's) and potentially indicates preference for drier and/or more open habitats than those at Csákvár. Polgárdi has an MN 13 mammal correlation and thus is younger than Csákvár. Consequently, the slightly more slender Polgárdi MP III's may be the result of a trend towards somewhat drier habitats.

Baltavár

Baltavár (MN 13) appears to have been mostly dominated by a single species of hipparion smaller than *Hippotherium primigenium* from Höwenegg and specimens from Csákvár and Polgárdi provisionally assigned to *"Hippotherium"* cf. *brachypus*. Kretzoi (Bernor, 2001) has applied the name *Hipparion microdon* KRETZOI 1985(?) to the Baltavár hipparion and a unique specific designation for the Baltavár hipparion would appear in order given that it is clearly distinct from hipparions from Rudabánya, Sümeg, Csákvár, and Polgárdi. The Baltavár hipparion also appears to group with other forms with short and broad MP III's generally assigned to the genus *Hippotherium* (as opposed to *Cremohipparion* or *Hipparion* which in general appear to have more elongate and/or slender in MP III's). Thus, the nomen *"Hippotherium" microdon* is applied to the majority of the Baltavár material. The larger MT III, MAFI Ob 3209/1, is considered as probably more closely related to forms from Csákvár and Polgárdi provisionally considered *"Hippotherium"* cf. *brachypus*. The mean habitat scores for *Hippotherium microdon* were negative suggesting a woodland or forest habitat for *Hippotherium microdon*.

Kislang

By MN 16, a large hipparion clearly adapted to more open habitats is recorded at Kislang. The habitat score of 1.06 for the single Kislang MT III included in this study strongly contrasts with the generally negative habitat scores for specimens from earlier Hungarian sites.

Mont Luberon

Mont Luberon (France) is the type locality of *Hipparion prostylum* and is correlated to MN 12. MT III's analyzed here from Mont Luberon appear variable in size

and relative elongation and this variation could be used to justify two species. However, the conservative approach of retaining all specimens from Mont Luberon in a single species is preferred until such time as evidence from other elements or increased sampling supports more than one species at Mont Luberon.

As noted earlier, *Hipparion prostylum* MP III's compare closely with those of *Cremohipparion mediterraneum* from Pikermi. This is a good example of what appears to be homoplasy with respect to hipparion MP III's. Thus, while differences in morphology are evident between different hipparion species and can certainly be used to recognize species level differences, it would seem certain that homoplasy in MP III morphology makes using MP III's as evidence regarding higher level systematics is problematic and should be used cautiously. Recognition of homoplasy in MP III's is, however, important in substantiating that MP III morphology is correlated with habitat.

The mean habitat scores for *Hipparion prostylum* from Mont Luberon were 0.25 for MC III's and 0.13 for MT III's. These scores are not so positive as to suggest an open environment where grazing would be the main dietary option. They do however suggest that *Hipparion prostylum* was certainly not tied to forested habitats.

Fossil hipparionines of Turkey, Iran, Afghanistan, Kazakhstan, and Pakistan

Sinap Formation

The four species from the Sinap Formation described by Bernor et al. (2003b) and analyzed ranged across the spectrum of habitat scores. MT III's of *"Hipparion" kecigibi* resulted in the lowest mean habitat score (= -0.83) for the Sinap Formation and MC III's of *"Hipparion" uzunagizli* resulted in the highest mean habitat score (= 0.98) for the Sinap Formation. *Cormohipparion sinapensis* had the next lowest habitat scores after *"Hipparion" kecigibi*. A fourth form, *"Hipparion"* sp. (Cursorial) of Bernor et al.

(2003b), had positive habitat scores intermediate between those of *Cormohipparion sinapensis* and *"Hipparion" uzunagizli*. Thus, it appears that the hipparions of the Sinap Formation were diverse and occupied a variety of niches.

As noted previously (Bernor et al., 2003b), the earliest Sinap localities appear to include only *Cormohipparion sinapensis* with increasing hipparion diversity and abundance at later localities (Bernor et al., 2003b; Scott et al., 2003). Locality 12 of the Sinap Formation dated to 9.6 Ma (Kappelman et al., 2003a) is known for the hominoid, *Ankarapithecus* (Alpagut et al., 1996), and includes MP III's attributed to all four species noted above and possibly a fifth large species (see Tables 11.1 and 11.12 in Bernor et al., 2003b). Thus, the diversity of habitats that appear likely for the Sinap hipparions do not appear to be in a strict temporal succession but at locality 12 the hipparion fauna appears to have sampled habitats from closed to open.

"Hipparion" kecigibi may have exploited more forested habitats or as suggested by Bernor et al. (2003b) hilly areas with rocky and uneven substrates. The alternative interpretation of negative habitat scores as indicators of such hilly and rocky habitats is supported by the fact that bovids assigned to the mountain habitat category also have negative habitat scores. *"Hipparion" uzunagizli* also found at locality 12 appears to have most likely been an open habitat specialist. *"Hipparion"* sp. (Cursorial) and *Cormohipparion sinapensis* likely utilized more intermediate habitats.

Esme Akçaköy

A single hipparion species appears probable for the MN 9 site of Esme Akçaköy (Turkey) and is referred to as *"Hipparion"* sp. (Esme Akçaköy) here. The Esme Akçaköy MT III's appear similar to those of *Cormohipparion sinapensis* and a close relationship with *Cormohipparion sinapensis* is possible. The habitat scores for Esme Akçaköy are intermediate and suggest intermediate habitats.

Akkaşdağı

The situation at Akkaşdağı (Turkey) parallels that at Sinap locality 12 in terms of hipparion diversity. Fours species are present (Koufos & Vlachou, in press; Scott & Maga, in press) and they appear to have had a range of habitat preferences. Overall, the younger Turolian Akkaşdağı hipparion species have more positive habitat scores than the Vallesian Sinap hipparions and none of the Akkaşdağı species would appear likely to have been forest dwelling like *Hippotherium primigenium* from Höwenegg. A temporal trend towards more open and/or drier habitats would appear likely based on the comparison of Sinap and Akkaşdağı. The high level of hipparion diversity is marked at both sites and hipparion diversity does not appear to have declined with any environmental changes.

Each of the four Akkaşdağı species appears likely to have specialized on a different portion of a habitat spectrum likely ranging from less open to more open environments. The larger bodied *"Hippotherium"* cf. *brachypus* and smaller bodied *Cremohipparion moldavicum* likely occupied the least open habitats of the Akkaşdağı hipparionines while *Hipparion* cf. *dietrichi* and *"?Plesiohipparion"* cf. *longipes* appear to have occupied more open habitats. *"?Plesiohipparion"* cf. *longipes* also appears to have been more extreme than *Hipparion* cf. *dietrichi*. The MT III habitat scores for *Cremohipparion moldavicum* and *"Hippotherium"* cf. *brachypus* are quite close to each other suggesting the possibility that they used the same habitat. The very different body size for these two species may suggest niche diversification along body size lines.

Çalta

Çalta is much younger than Akkaşdağı and has been correlated to MN 15 (Mein, 1990). Two hipparion species are recognized from Çalta: a gracile one and a robust form. The robust form is *Hipparion heintzi* and the type specimens or this species is the MC III

ACA49a from Çalta (Eisenmann & Sondaar, 1998). The gracile form is referred to "*?Plesiohipparion*" cf. *longipes* (Eisenmann & Sondaar, 1998). The classification of the Çalta material into two species is confirmed by the analysis conducted here. The complete MT III from Çalta referred to "*?Plesiohipparion*" cf. *longipes* plots just outside the 95% confidence ellipse for PC1 versus MGSV of the MT III's from Akkaşdağı referred to "*?Plesiohipparion*" cf. *longipes* (Koufos & Vlachou, in press) (fig. 6.23A).

Hipparion heintzi has broad and short MP III's in sharp contrast with "*?Plesiohipparion*" cf. *longipes*. Not surprisingly, the habitat scores for these two species are divergent. The "*?Plesiohipparion*" cf. *longipes* MT III had a habitat score of 0.50 suggesting open and/or dry habitats. The mean habitat score for *Hipparion heintzi* was 0.16 based on MC III's and -0.31 based on MT III's.

Eisenmann and Sondaar (1998) noted that the morphology of the *Hipparion heintzi* MP III's would usually suggest humid environments but that other evidence for a steppe environment at Çalta rules out his interpretation. Instead, it was suggested that the MP III morphology of *Hipparion heintzi* is convergent with that of MP III's of hipparions from more humid and forested environments and that it represents adaptation to soft soil indicated by the presence of burrowing rodents at Çalta (Eisenmann & Sondaar, 1998). The connection between *Hipparion heintzi* MP III morphology and soft soil is reasonable but it is also worth noting that the habitat scores for *Hipparion heintzi* are not really that low and would not be interpreted here as indicative of very humid or forested habitats. The case of *Hipparion heintzi* represents an important example of the problems with overweighting interpretations based simply on morphology. It seems certain that morphology generally associated with certain conditions (e.g., humid and forested environments) might also arise under other conditions (e.g., rocky and difficult terrain, soft soil, or sandy substrates).

Siwaliks

Most of the MP III's from the Siwaliks analyzed here were MT III's and these specimens were divided into three size groups. The four smallest of these MT III's were clearly relatively elongate and slender and three of these specimens have been considered *"Hipparion" antelopinum* FALCONER & CAUTLEY 1849 previously (Bernor & Scott, 2003). All four of these smaller, more slender and elongate MT III's and the smaller of the two MC III's analyzed here are retained in *"Hipparion" antelopinum*.

Four larger MT III's are relatively short and broad and three of these were referred to as *Sivalhippus perimense* PILGRIM 1910 (Bernor & Scott, 2003). All four of these specimens are considered as probably belonging to *Sivalhippus perimense* here. One MC III analyzed here is relatively short and broad also referred to *Sivalhippus perimense*.

Two remaining MT III's were some what larger than those already discussed probably belonging to *Sivalhippus perimense*. One of these, GSP 17774, is possibly a large individual of *Sivalhippus perimense*. The other quite large MT III, GSP 50353, is more elongate and slender than GSP 17774 and is referred to here as *"Hipparion"* sp. (Siwaliks).

The mean habitat score for *"Hipparion" antelopinum* was 0.35 compared to -0.91 for the four MT III's most securely attributed to *Sivalhippus perimense*. Thus, two Siwalik species with likely contrasting habitat preferences are represented here. *Sivalhippus perimense* is a candidate for a forest adapted form and has a similar habitat score as that of *Hippotherium primigenium* from Höwenegg. *"Hipparion" antelopinum* would likely have use intermediate environments. One of the *"Hipparion" antelopinum* MT III's is from the hominoid locality Y0311 and the inference of intermediate habitats

for *"Hipparion" antelopinum* is consistent with the interpretation of the Y0311 paleoenvironment based on analysis of bovid femora made previously (Scott et al., 1999).

Molayan

Molayan (Afghanistan) has been dated to MN 12 (Sen, 1998) and is the type site of *Hipparion molayanense* ZOUHRI 1996. *Hipparion molayanense* is described as hypsodont with slender metapodials (Zouhri, 1996). These characters would generally suggest a grazing form adapted to more open and dry habitats. The results of this analysis do in fact confirm that *Hipparion molayanense* does in fact have elongate MT III's for its size. However, it also appears that the Molayan MP III's are not relatively slender for their size (fig. 6.26A). This translates into a fairly low mean habitat score of -0.34 for the *Hipparion molayanense* MT III's. This score is not low enough to indicate forested habitats (it is no as low as that of *Hippotherium primigenium* from Höwenegg) but does suggest at least seasonally wet habitats or the reliance on some wooded areas.

A study of intra- and inter-tooth carbon and oxygen isotopes for molars of *Tragoportax* from Molayan suggested a single birth season prior to a hot/dry season for *Tragoportax* and was interpreted to support an open and dry environment for *Tragoportax* at Molayan (Zazzo et al., 2002). Thus, the negative habitat scores seem to be at odds with other evidence regarding the paleoenvironmental conditions at Molayan. The Molayan MT III's were subject to some postdepositional deformation and despite efforts to not record measurements that were likely distorted it is possible that the apparently great relative breadth for the Molayan MT III's was influenced by postdepositional deformation. It is considered more likely here that *Hipparion molayanense* specialized on an alternative niche to that of *Tragoportax*. One possibility would be a reliance on seasonally flooded areas which would explain the relatively broad diaphysis of the

Hipparion molayanense MT III's. This would be consistent with open habitats and a diet primarily of graze. Future study is needed to test this hypothesis.

Maragheh

Most of the MP III's from Maragheh come from the collections of the MNHN in Paris collected by R. de Mecquenem. Based on de Mecquenem's report (de Mecquenem, 1908), Bernor (1986) constrained the MNHN collections (including the primate *Mesopithecus pentelici*) to between -52 and -28 m below the Loose Chippings Tuff which correlates with Middle Maragheh (= -52 to -20 m below the Loose Chippings Tuff). The Loose Chippings Tuff has been radiometrically dated to 7.787 Ma and the Mirduq Tuff which is -110 m below the Loose Chipping Tuff has been radiometrically dated to 8.635 Ma (Swisher, 1996). Thus, based on an interpolated sedimentation rate Middle Margheh is constrained to between 8.2 and 8.0 Ma (Bernor et al., 1996c) and is considered MN 11 correlative.

Bernor (1986) reported three hipparion species from Middle Maragheh: *Hipparion prostylum*, *Cremohipparion* aff. *moldavicum*, and *Cremohipparion matthewi*. "*Hippotherium*" *brachypus* was added to this list later as a rare occurrence (Bernor et al., 1996c). The MT III from Middle Maragheh assigned to the Maragheh Large Morph compares very closely with "*Hippotherium" brachypus* from Pikermi and with "*Hippotherium"* cf. *brachypus* from Akkaşdağı. The two MC III's from Middle Maragheh assigned to the Maragheh Large Morph appear intermediate between "*Hippotherium" brachypus* from Pikermi and "*Hippotherium"* cf. *brachypus* from Akkaşdağı. Thus, given the report of a rare occurrence of "*Hippotherium" brachypus* from Middle Maragheh, it is most reasonable to refer the three specimens assigned here to the Maragheh Large Morph to "*Hippotherium"* cf. *brachypus*.

Hipparion prostylum is considered an important biostratigraphic indicator and the first occurrence of *Hipparion prostylum* at Maragheh is correlative of basal MN 12 (Bernor et al., 1996a; Bernor et al., 1996c). The Maragheh MC III's are compared with those from Mont Luberon the type locality of *Hipparion prostylum* in figures 6.27 and 6.28. The Mont Luberon MC III's compare best with the Maragheh Small Morph in terms of size (fig. 6.27B) and relative elongation (fig. 6.28B). Similarly, the Mont Luberon MT III's are more similar in size to the Maragheh Small Morph (fig. 6.27A). Thus, referral of the Maragheh Small Morph specimens to *Hipparion* cf. *prostylum* would appear most appropriate.

Cremohipparion aff. *moldavicum* is represented by several skulls in the MNHN collection. Thus, it is likely that some or many MP III's from the MNHN collection are also derived from *Cremohipparion* aff. *moldavicum*. The Maragheh Elongate Morph MC III's compare closely with MC III's from Akkaşdağı assigned to *Cremohipparion* cf. *moldavicum* in terms of relative elongation and relative slenderness (fig. 6.28B) and can tentatively be considered as *Cremohipparion* aff. *moldavicum*. However, these specimens are larger than those of *Cremohipparion* cf. *moldavicum* from Akkaşdağı and larger than the Maragheh Small Morph (= *Hipparion* cf. *prostylum*) (fig. 6.27B). Thus, based on MP III's it would appear that *Cremohipparion* aff. *moldavicum* from Middle Maragheh is larger than *Hipparion prostylum*. It is not clear that other occurrences of *Cremohipparion moldavicum* are of a species as large as *Cremohipparion* aff. *moldavicum* from Middle Maragheh.

One MT III and one MC III from the MNHN Middle Maragheh sample were assigned to the Maragheh Dwarf Morph. The three MT III's from Maragheh in general all compared closely with those of *Cremohipparion matthewi* from Samos. Since *Cremohipparion matthewi* has also been reported for Middle Maragheh it is most

reasonable to assign the Maragheh Dwarf Morph MP III's to *Cremohipparion* cf. *matthewi*.

The provenience of the two MC III's which were assigned to the Maragheh Broad Morph is not certain at this time and little more can be said of them. They resulted in a very low mean habitat score of -1.38 suggesting the possibility of a forest-adapted hipparion distributed somewhere in the Maragheh faunal succession.

The four likely species from Middle Maragheh based MP III's had mean habitat scores distributed from strongly positive to slightly negative. Mean habitat scores for *Cremohipparion* aff. *moldavicum* of 0.83 (MC III's) and 0.72 (MT III's) suggest open habitats. The scores for "*Hippotherium"* cf. *brachypus* and *Hipparion* cf. *prostylum* were lower and suggest more intermediate woodland or broken cover habitats. *Cremohipparion* cf. *matthewi* is not so well sampled and the MC III and MT III mean habitat scores varied from 0.31 (MC III's) to 1.33 (MT III's). Thus, *Cremohipparion* cf. *matthewi* might have specialized on fairly open or more intermediate habitats.

Kalmakpai

The specimen of *Hipparion* cf. *elegans* from Kalmakpai (Kazakhstan) analyzed here had a very positive habitat score and likely utilized open habitats.

Fossil hipparionines of Africa

Bou Hanifia

The three MT III's from Bou Hanifia which are referred to *"Hippotherium" africanum* (Bernor & Scott, 2003) were already discussed in conjunction with the Can Llobateres hipparions. The mean habitat score of 0.17 and mammal correlation of either upper MN 9 or basal MN 10 makes *"Hippotherium" africanum* among more open adapted examples of the *Hippotherium primigenium* Complex in the Vallesian. It would

appear that *"Hippotherium" africanum* was adapted to intermediate habitats in terms of cover.

Sahabi

The Sahabi hipparions have already been discussed in greater depth previously (Bernor & Scott, 2003). The slender MC III of *Cremohipparion* aff. *matthewi* (Bernor & Scott, 2003) from Sahabi had a positive habitat score of 1.07 supporting the interpretation that *Cremohipparion* aff. *matthewi* used more open habitats (Bernor & Scott, 2003).

Lothagam

The slender and elongate MC III (= KNM-LT139A) from Lothagam belongs to *Eurygnatohippus feibeli* BERNOR & HARRIS 2003 (Bernor & Harris, 2003) and has a habitat score of 1.00 suggesting the use of open habitats.

One MT III (KNM-LT25470) and one MC III (KNM-LT22871) from Lothagam belonging to *Eurygnatohippus turkanense* HOOIJER & MAGLIO1973 had habitat scores of 0.13 and -0.71 respectively suggesting a habitat preference for forested areas or possibly intermediate woodland habitats.

Fossil hipparionines of North America

Christmas Quarry

As noted earlier, the North American Christmas Quarry MP III's are included here primarily to aid in the description of hipparionine MP III scaling. A full discussion of this sample is beyond the scope of this thesis.

General trends among late Miocene hipparionines

Sondaar (1971) has noted the tension between describing species that are morphologically discrete while at the same time avoiding a taxonomy in which each new site yields a new species. The right balance between these two extremes is important here

if trends and patterns in hipparion evolution and environments are to be discerned. In this study, the task of sorting MP III's purely on the basis of morphology with no reference to sites or geographic and temporal data would have been virtually impossible. Thus, the previous discussion has focused on discussion of specimens from each site included in the study as the starting point for analysis. However, it is also important to attempt to draw comparisons and contrasts between sites and attempt to define the occurrence of hipparions more broadly in time and space.

In various cases, the presence of the same species or closely related members of the same lineage has been proposed at different sites. For instance, *"Hippotherium"* cf. *brachypus* has been suggested for Pikermi, Akkaşdağı, Csákvár, Polgárdi, Baltavár, Maragheh, and Samos. The validity of a species can be assessed by comparing the variability of a proposed species with that observed for a standard thought to constitute a single species. Small sample sizes make this approach impractical in many cases and the previous discussion has relied mostly on visual comparisons between MP III's of interest and 95% confidence ellipses for the two standards used in this study, Höwenegg and La Roma 2. The three main variables used in sorting specimens were size (MGSV), relative length (siM1), and relative slenderness (siM3). The variability of proposed species can be evaluated formally by comparing their coefficients of variation (CV) for MGSV and variances for siM1 and siM3 to those same statistics for the La Roma 2 and Höwenegg standards. Cases where the CV for MGSV or the variances for siM1 and siM3 are greater that those observed for the single species standard are more likely to include multiple species. It is, however, important to note that the more comparisons that are made the more likely there are to be indications suggesting multiple species. It is also true that conspecifics from different localities should be assumed to generate samples with more variability than single site samples where not only a single species but a single population

is likely. Thus, the comparisons made here between proposed single species groups and the comparative standards need to be sensitive to these factors.

Comparisons were made between the CV of MGSV, the variance of siM1, and the variance of siM3 for MP III's that were referred to a common species (including cases where the open nomenclature "cf." was used) and the greater value for each of these statistics from either the La Roma 2 or the Höwenegg standard. Cases where variability observed for the most variable of the standards was exceeded in the case of two or more of the three statistics compared for both MC III's and MT III's were considered as likely indicating more than one species. These comparisons were only made in the case where there were samples of at least five MC III's or 5 MT III's and the sample in question spanned more than one site. The results of these comparisons are shown in table 6.9.

MP III's referred to *"Hippotherium"* cf. *brachypus* from Akkaşdağı, Baltavár, Csákvár, Maragheh, Pikermi, Polgárdi, and Samos appear to plausibly belong to the same species on the basis of MP III morphology. In particular, the 18 MC III's from these sites assigned to *"Hippotherium"* cf. *brachypus* than either the Höwenegg of La Roma 2 standard in terms of size and relative slenderness.

In contrast to the case of *"Hippotherium"* cf. *brachypus*, MP III's assigned to *Hippotherium* cf. *primigenium* from Höwenegg, Dorn-Dürkheim, Eppelsheim, Esselborn, Charmoille, and Ravin de la Pluie appear more likely to be divisible into multiple species according to the criteria described above. The Charmoille specimens for example might be referred to a smaller variant of *Hippotherium primigenium*.

Hipparion cf. *prostylum* from Maragheh and Mont Luberon also failed to meet the test for a single species. This may be due less to variation between the Maragheh sample and the Mont Luberon sample and more to variation within the two samples. For instance, it has already been noted that the Mont Luberon MT III's are variable in size

and morphology and could include a second form in addition to *Hipparion prostylum*. It seems likely that some of the Mont Luberon MP III's are conspecific with those from Maragheh assigned to *Hipparion* cf. *prostylum* here.

Specimens from Akkaşdağı and Samos assigned to *Hipparion* cf. *dietrichi* also failed to meet the test for a single species. *Hipparion dietrichi* remains problematic due to the difficulty of securely associating postcrania from Samos with skulls from Samos of *Hipparion dietrichi*.

While the sampling is still low, five MT III's and five MC III's from Inzersdorf, Prottes, and Schwechat which were assigned to *"Hipparion"* sp. 1 (Vienna Basin) can reasonably be interpreted as possible conspecifics on the basis of MP III size and morphology (tab. 6.9). It would appear that the Vienna Basin records at least one species of hipparion different from both *Hippotherium primigenium* and other hipparions from farther east of the Pannonian Basin in Hungary.

Hipparion melendezi, *"Hippotherium"* cf. *catalaunicum*, *Cremohipparion* cf. *matthewi* were too poorly sampled (N < 5) for either the MT III or MC III to make any judgements regarding their validity as single species'. *"?Plesiohipparion"* cf. *longipes* nominally was from Çalta and Akkaşdağı but only one MT III was from Çalta and thus it is impossible to make any firm characterization regarding the conspecificity of *"?Plesiohipparion"* cf. *longipes* from Çalta and Akkaşdağı.

There are a few general trends worth noting here. First, hipparion diversity appears to be a somewhat regional phenomenon. For example, Central European sites typically preserve a single species of hipparion (e.g., Höwenegg, Charmoille). This also appear to be more or less the trend in the Vienna Basin where for instance there appears to be a single species at Inzersdorf.

In contrast with Central Europe, the circum-Mediterranean area appears much more diverse. Sites in Greece typically record two or three species of hipparion. This is true earlier in time at the MN 10 locality of Ravin de la Pluie as well as at younger localities (e.g., Pikermi, Samos). Maragheh is similarly speciose. Turkish localities record multiple species of hipparion from as early as upper MN 9 (locality 91 and locality 12 of the Sinap Formation) to later times (e.g., Akkaşdağı).

Vallesian sites in Spain appear to be possibly more diverse than those in Central Europe. Two species are possible at Can Llobateres and the similarly aged site of Santiga preserves a third species of hipparion not found at Can Llobateres as well as possibly a rare larger species. Spanish sites inland from Can Llobateres appear less speciose: Los Valles de Fuentidueña (MN 9) and La Roma 2 (MN 10) each preserve only single species of hipparion. Notably, both of these species appear adapted to open habitats. This is contra the model of de Bonis (1999) linking open environments to greater equid diversity.

Sites of the Pannonian Basin in Hungary often appear to record two species of hipparion. For example, Baltavár appears dominated by one form but also may preserve a rarer second and larger species. Csákvár almost certainly includes two species.

A second general observation regards temporal trends in diversity and apparent habitat. First, older localities do preserve hipparions that quite likely used open habitats. Examples include *Hipparion melendezi* from Los Valles de Fuentidueña (MN 9), *"Hipparion"* sp. (La Roma 2) from La Roma 2, and *"Hipparion" uzunagizli* from upper MN 9 in the Sinap Formation. Thus, a smooth transition from uniformly more forested habitats to more open and dry habitats from Vallesian to Turolian times is not supported. It is worth noting that in general younger sites do tend to preserve hipparions with more positive habitat scores. Thus, while the Pikermi and Akkaşdağı MP III's assigned to *"Hippotherium"* cf. *brachypus* are reasonably accommodated in a single species here it is

also true that the younger Akkaşdağı specimens result in higher habitat scores suggesting directional selection for more open habitats.

It also appears that diversity does not simply increase from the Vallesian to the Turolian. For instance, Baltavár appears dominated by a single species (although a second may be present and rare) while the Vallesian site of Rudabánya preserves two hipparion species. Similarly, the Turolian site of Piera (MN 11) in Spain appears to include one species of hipparion while the MN 9 locality of Can Llobateres likely included two species. The early occurrences of more multiple hipparion species at a single site indicates either multiple immigrant species from the New World and/or the rapid diversification of the clade. The case of the Sinap Formation appears to imply the latter (Bernor et al., 2003b; Scott et al., 2003).

A final general observation regards the fairly common instance of hipparion species distinguished at a site not based only on size but on morphology as well. For example, Pikermi preserves both *"Hippotherium" brachypus* and *Cremohipparion mediterraneum.* Difference in size alone would be enough to distinguish these two species at Pikermi but it also appears that they are distinct in morphology related to habitat and that it is likely they preferred different habitats. Thus, hipparion diversity appears linked to habitat variability. Other examples of the co-occurrence of such "contra-morphs" (species with morphology suggesting contrasting habitats) include *Sivalhippus perimense* and *"Hipparion" antelopinum* in the Siwaliks, *"Hipparion" kecigibi* and *"Hipparion" uzunagizli* at Sinap, and *Cremohipparion macedonicum* and *Hippotherium* cf. *primigenium* at Ravin de la Pluie. In fact, the existence of "contra-morphs" at a site seems to be more common than the occurrence of two species separated mainly by size.

Cases where hipparion species appear to be distinguished mainly by size as opposed to morphology typically seem to occur more often at very speciose sites. Thus, at Akkaşdağı four species are present including "contra-morphs." However, *Cremohipparion moldavicum* and *"Hippotherium" brachypus* have similar habitat scores but are different in size. A general rule would appear that hipparion species diversity first implies species using different habitat types (as assessed by MP III morphology) and it is only at larger species numbers (three or four) that size appears to differentiate species that have the same basic MP III morphology. Thus, a general rule of thumb would be that hipparion diversity implies habitat diversity.

The framework outlined here provides some evidence regarding habitats of hipparions from various late Miocene sites and the presence of various hipparion habitats informs on the general paleoenvironments present at various sites. This in turn informs on the paleoecology of hominoids at different sites. The problem of small sample sizes at specific sites makes some conclusions necessarily more tentative than others. However, hipparion MP III's are well-preserved by and large and provide much more robust samples than for instance bovid metapodials or hipparion cranial material. Future work is needed to integrate the postcranial evidence generally reflecting substrate and cover variables for hipparions discussed here with dietary evidence for the same hipparions. Other important questions concern the abundance of hipparions at sites relative to other taxa.

Table 6.1: Least squares regression statistics for morphological variables versus size for fossil hipparionines.

Element	Variable*	Intercept	Slope	*df*	R^2	*P*	95% Confidence Interval of the Slope	95% Confidence Interval of the Intercept
MT III	M1	1.6541	-0.5031	288	0.5167	<0.0001	-0.5596 - -0.4467	1.5705 - 1.7377
MT III	M3	-0.2269	0.1224	288	0.0721	<0.0001	0.0715 - 0.1734	-0.3024 - -0.1514
MT III	M4	0.0971	-0.1036	288	0.0733	<0.0001	-0.1463 - -0.0609	0.0338 - 0.1603
MT III	M5	0.0768	0.0238	288	0.0062	0.1812	-0.0111 - 0.0587	0.025 - 0.1285
MT III	M6	0.0468	-0.0186	288	0.0014	0.5197	-0.0754 - 0.0382	-0.0373 - 0.1309
MT III	M10	-0.0530	0.0952	288	0.0855	<0.0001	0.0591 - 0.1313	-0.1065 - 0.0005
MT III	M11	-0.0334	0.0625	288	0.0514	0.0001	0.0314 - 0.0936	-0.0795 - 0.0127
MT III	M12	0.0107	-0.0143	288	0.0021	0.4377	-0.0505 - 0.0219	-0.043 - 0.0644
MT III	M13	0.0125	-0.0818	288	0.0636	<0.0001	-0.1182 - -0.0454	-0.0414 - 0.0664
MT III	M14	0.0695	-0.0856	288	0.0804	<0.0001	-0.1192 - -0.052	0.0198 - 0.1192
MC III	M1	1.8210	-0.6487	215	0.5662	<0.0001	-0.7251 - -0.5724	1.7104 - 1.9317
MC III	M3	-0.2060	0.1307	215	0.0551	0.0005	0.058 - 0.2034	-0.3114 - -0.1006
MC III	M4	0.1154	-0.1585	215	0.0768	<0.0001	-0.2323 - -0.0846	0.0084 - 0.2225
MC III	M5	0.0301	0.0657	215	0.0461	0.0015	0.0255 - 0.1059	-0.0281 - 0.0883
MC III	M6	0.0046	-0.0246	215	0.0027	0.4449	-0.088 - 0.0388	-0.0873 - 0.0965
MC III	M10	-0.1475	0.1759	215	0.1926	<0.0001	0.1275 - 0.2244	-0.2177 - -0.0773
MC III	M11	-0.0823	0.1148	215	0.1081	<0.0001	0.0704 - 0.1591	-0.1465 - -0.018
MC III	M12	0.0824	-0.0663	215	0.0361	0.0050	-0.1124 - -0.0202	0.0157 - 0.1492
MC III	M13	0.1184	-0.1446	215	0.1181	<0.0001	-0.1977 - -0.0915	0.0414 - 0.1954
MC III	M14	0.0848	-0.0931	215	0.0746	<0.0001	-0.1371 - -0.049	0.0209 - 0.1487

*Variables are the tabled measurement from Eisenmann (1988) divided by the size variable MGSV and logged. Regression statistics are for these variables regressed against $\log_{10}$(MGSV).

Table 6.2: Eigenvalues for Principal Components Analysis (PCA) of MT III and MC III.

Element	Principal Component	Eigenvalue	% Variance Explained
MT III	One	0.00139475	30.14%
MT III	Two	0.00093323	20.17%
MT III	Three	0.00068671	14.84%
MT III	Four	0.00052006	11.24%
MT III	Five	0.00033417	7.22%
MT III	Six	0.00023920	5.17%
MT III	Seven	0.00022858	4.94%
MT III	Eight	0.00015887	3.43%
MT III	Nine	0.00013175	2.85%
MT III	Ten	0.00000003	0.00%
MC III	One	0.00139011	35.61%
MC III	Two	0.00072060	18.46%
MC III	Three	0.00051394	13.17%
MC III	Four	0.00036710	9.40%
MC III	Five	0.00025151	6.44%
MC III	Six	0.00023491	6.02%
MC III	Seven	0.00018222	4.67%
MC III	Eight	0.00013094	3.35%
MC III	Nine	0.00011185	2.87%
MC III	Ten	0.00000014	0.00%

Table 6.3: Eigenvectors for Principal Components Analysis (PCA) of MT III and MC III.

		Eigenvector			
Element	**Variable**	**Principal Component One (PC1)**	**Principal Component Two (PC2)**	**Principal Component Three (PC3)**	**Principal Component Four (PC4)**
MT III	siM1	0.601	0.225	0.405	0.416
MT III	siM3	-0.537	-0.027	0.455	-0.225
MT III	siM4	0.218	0.104	0.594	-0.347
MT III	siM5	-0.024	-0.120	-0.022	0.505
MT III	siM6	0.333	-0.835	-0.067	-0.088
MT III	siM10	-0.278	0.007	-0.071	0.378
MT III	siM11	-0.187	0.123	-0.025	0.329
MT III	siM12	0.212	0.376	-0.202	-0.125
MT III	siM13	0.145	0.158	-0.382	-0.346
MT III	siM14	0.117	0.213	-0.281	-0.082
MC III	siM1	0.600	0.201	0.054	
MC III	siM3	-0.491	0.450	0.034	
MC III	siM4	0.443	0.606	-0.261	
MC III	siM5	0.057	-0.080	0.074	
MC III	siM6	-0.395	-0.817	0.118	
MC III	siM10	-0.271	0.152	0.064	
MC III	siM11	-0.213	-0.003	0.056	
MC III	siM12	0.220	-0.266	0.242	
MC III	siM13	0.148	-0.343	0.250	
MC III	siM14	0.104	-0.123	0.356	

Table 6.4: Mean habitat scores for fossil hipparionines by site and possible species.

		MC III			MT III		
Site	**Species**	***N***	**X**	**SD**	***N***	**X**	**SD**
Los Valles de Fuentidueña	*Hipparion melendezi*	1	0.95		4	0.74	0.16
El Lugarejo	*Hipparion melendezi*	2	0.44	0.24	1	0.40	
Santiga	*"Hipparion"* cf. *depereti*	4	-1.01	0.66	4	-1.06	0.39
Can Llobateres	*"Hippotherium"* aff. *catalaunicum* (Can Llobateres)	3	0.10	0.29	3	-0.43	0.19
Can Llobateres	*"Hippotherium"* cf. *catalaunicum*	1	-0.55				
Polinya	*"Hippotherium"* aff. *catalaunicum*	1	-0.14				
La Tarumba	*"Hippotherium"* aff. *catalaunicum*	1	-0.10				
Piera	*"Hippotherium"* aff. *catalaunicum* (Piera)	6	-0.27	0.58	2	0.14	0.55
La Roma 2	*"Hipparion"* sp. (La Roma 2)	7	0.85	0.36	16	0.89	0.38
Concud	*Hipparion concudense*	7	-0.29	0.77	6	-0.59	0.51
La Gloria 4	*Hipparion* cf. *elegans*				1	1.27	
Ballestar	*"Hippotherium"* aff. *catalaunicum*				1	0.10	
Venta del Moro	*Hipparion* sp. (Venta del Moro)	2	0.77	0.03	1	0.97	
Layna	*Hipparion fissurae*				1	-0.36	
Pikermi	*"Hippotherium" brachypus*	2	-0.53	0.70	6	-0.57	0.86
Pikermi	*Cremohipparion mediterraneum*	3	0.77	0.25	5	0.32	0.97
Samos	*"Hipparion"* cf. *proboscideum*	3	-0.15	0.64	4	-0.38	0.88
Samos	*"Hippotherium"* cf. *brachypus*	1	-0.36				
Samos	*"Hippotherium"* cf. *giganteum*				4	1.62	0.83
Samos	*Cremohipparion matthewi*				4	0.15	0.99
Samos	*Hipparion* cf. *dietrichi*	5	-0.11	0.38	6	0.04	0.45
Samos	*Hipparion* sp. SONDAAR 1971	4	-0.12	0.60	1	-0.22	
Samos	*'Hipparion"* sp. (Quarry 6, Samos)	1	-0.90				
Ravin de la Pluie	*"Hipparion"* aff. *depereti*				1	0.09	
Ravin de la Pluie	*Cremohipparion macedonicum*				1	1.32	
Ravin de la Pluie	*Hippotherium primigenium*				1	-0.31	

Saloniki	*"Hipparion"* sp. 1 (Saloniki)	1	-0.54				
Saloniki	*"Hipparion"* spp. (Saloniki)	1	0.96		4	1.15	1.01
Maramena	*Cremohipparion* cf. *matthewi*				2	0.35	0.04
Höwenegg	*Hippotherium primigenium*	14	-0.99	0.34	20	-0.74	0.63
Eppelsheim	*Hippotherium primigenium*	1	0.09		1	0.87	
Esselborn	*Hippotherium primigenium*				2	-0.43	0.40
Dorn-Dürkheim	*Hippotherium kammerschmitti*	1	-0.07				
Dorn-Dürkheim	*Hippotherium primigenium*				2	-1.01	1.01
Charmoille	*Hippotherium* cf. *primigenium*	2	-1.53	0.11	3	-0.66	0.48
Inzersdorf	*"Hipparion"* sp. 1 (Vienna Basin)	4	-0.58	0.52	4	-1.06	0.82
Prottes	*"Hipparion"* sp. 1 (Vienna Basin)				1	-0.06	
Gols	*"Hipparion"* sp. 2 (Vienna Basin)	1	-0.65				
Gols	*"Hipparion"* sp. 3 (Vienna Basin)	1	0.49				
Schwechat	*"Hipparion"* sp. 1 (Vienna Basin)	1	-0.28				
Sümeg	*Hippotherium sumegense*	1	-1.31				
Csákvár	*"Hippotherium"* cf. *brachypus*	2	0.14	0.60	2	-0.40	0.07
Csákvár	*Hippotherium* cf. *intrans*	1	-0.65				
Polgárdi	*"Hippotherium"* cf. *brachypus*	2	0.10	0.07	2	0.04	0.07
Baltavár	*"Hippotherium"* cf. *brachypus*				1	-0.68	
Baltavár	*Hipparion microdon*	9	-0.42	0.43	8	-0.09	0.56
Kislang	*"Plesiohipparion" moritorum*				1	1.07	
Mont Luberon	*Hipparion prostylum*	4	0.25	0.53	7	0.13	0.71
Sinap	*"Hipparion" kecigibi*	5	-0.45	0.48	5	-0.83	0.62
Sinap	*"Hipparion"* sp. (Upper Sinap)	1	0.51		1	1.03	
Sinap	*"Hipparion"* sp. 1 (Cursorial Morph)	2	0.60	0.85	5	0.27	0.80
Sinap	*"Hipparion" uzunagizli*	1	0.98		2	0.89	0.08
Sinap	*Cormohipparion sinapensis*	2	-0.30	0.11	4	-0.53	0.48
Sinap	*indet. indet.*	2	-0.16	1.41			
Esme Akçaköy	*"Hipparion"* sp. (Esme Akçaköy)	4	0.27	0.66	7	-0.12	0.59
Akkaşdağı	*"?Plesiohipparion"* cf. *longipes*	8	1.19	0.42	12	0.79	0.64
Akkaşdağı	*"Hippotherium"* cf. *brachypus*	5	0.36	0.41	6	0.14	0.27
Akkaşdağı	*Cremohipparion* cf. *moldavicum*	14	0.51	0.56	15	0.29	0.44
Akkaşdağı	*Hipparion* cf. *dietrichi*	6	0.36	0.53	15	0.64	0.61
Çalta	*"?Plesiohipparion"* cf. *longipes*				1	0.50	

Çalta	*Hipparion heintzi*	5	0.16	0.51	2	-0.31	0.35
Siwaliks	*"Hipparion" antelopinum*	1	0.58		4	0.35	0.57
Siwaliks	*"Hipparion"* sp. (Siwaliks)				1	0.44	
Siwaliks	*"Sivalhippus"* cf. *perimense*				1	-1.76	
Siwaliks	*"Sivalhippus" perimense*	1	0.32		4	-0.91	0.45
Molayan	*Hipparion molayanense*				5	-0.34	0.63
Maragheh	*"Hipparion"* sp. (Maragheh)	2	-1.38	0.41			
Maragheh	*"Hippotherium"* cf. *brachypus*	2	0.07	1.49	1	-0.33	
Maragheh	*Cremohipparion* aff. *moldavicum*	10	0.83		8	0.72	0.93
Maragheh	*Cremohipparion* cf. *matthewi*	4	0.31	0.83	3	1.33	0.42
Maragheh	*Hipparion* cf. *prostylum*	7	0.33	0.38	3	0.33	0.25
Kalmakpai	*Hipparion* cf. *elegans*				1	1.02	
Bou Hanifia	*"Hippotherium" africanum*				3	0.17	0.35
Sahabi	*"Cremohipparion"* aff. *matthewi*	1	1.07				
Lothagam	*Eurygnatohippus feibeli*	1	1.00				
Lothagam	*Eurygnatohippus turkanense*	1	-0.71		1	0.13	
Christmas Quarry	*Cormohipparion occidentale* Medium	7	-0.84	0.65	20	-0.84	0.45

Key: *N*, sample size; X, mean habitat score; SD, standard deviation.

Table 6.5: Mean principal component scores for fossil hipparionines by site and possible species.

		MC III PCA				MT III PCA			
Site	**Species**	***N***	**PC1**	**PC2**	**PC3**	***N***	**PC1**	**PC2**	**PC3**	**PC4**
Los Valles de Fuentidueña	*Hipparion melendezi*	1	0.47	-0.54	0.45	4	0.60 (0.32)	0.02 (0.49)	-0.85 (0.76)	0.33 (0.28)
El Lugarejo	*Hipparion melendezi*	2	0.07 (0.13)	-0.78 (0.61)	1.01 (0.77)	1	0.34	0.42	-0.81	0.52
Santiga	*"Hipparion"* cf. *depereti*	4	-1.57 (0.44)	0.32 (0.60)	-0.12 (0.50)	4	-1.14 (0.25)	-0.60 (0.54)	-0.44 (0.88)	-0.31 (0.56)
Can Llobateres	*"Hippotherium"* aff. *catalaunicum* (Can Llobateres)	3	-0.45 (0.43)	-0.68 (0.65)	1.21 (0.28)	3	-0.88 (0.22)	-0.33 (0.93)	-0.67 (0.66)	0.17 (0.25)
Can Llobateres	*"Hippotherium"* cf. *catalaunicum*	1	-0.65	0.19	0.48					
Polinya	*"Hippotherium"* aff. *catalaunicum*	1	-1.07	-0.66	-0.11					
La Tarumba	*"Hippotherium"* aff. *catalaunicum*	1	-1.02	-1.57	1.42					
Piera	*"Hippotherium"* aff. *catalaunicum* (Piera)	6	-0.83 (0.38)	-1.06 (0.81)	0.89 (1.08)	2	-0.26 (0.53)	-0.44 (0.12)	-0.96 (0.91)	0.26 (0.23)
La Roma 2	*"Hipparion"* sp. (La Roma 2)	7	0.96 (0.52)	-0.91 (0.55)	0.29 (0.89)	16	1.01 (0.38)	-0.44 (0.38)	-0.41 (0.68)	0.14 (0.59)
Concud	*Hipparion concudense*	7	-0.32 (0.61)	-0.04 (0.47)	0.22 (0.74)	6	-0.28 (0.48)	-0.01 (0.18)	0.45 (0.66)	-0.79 (0.72)
La Gloria 4	*Hipparion* cf. *elegans*					1	1.82	0.86	0.56	0.06
Ballestar	*"Hippotherium"* aff. *catalaunicum*					1	-0.63	-0.13	-1.04	1.67
Venta del Moro	*Hipparion* sp. (Venta del Moro)	2	0.69 (0.46)	-0.36 (0.12)	1.00 (0.04)	1	0.47	0.72	-1.05	0.57
Layna	*Hipparion fissurae*					1	0.73	1.44	2.30	-0.89

Pikermi	*"Hippotherium" brachypus*	2	-0.68 (0.33)	0.20 (2.64)	0.72 (1.47)	6	-0.49 (0.86)	-0.15 (0.46)	0.04 (0.90)	-1.38 (0.49)
Pikermi	*Cremohipparion mediterraneum*	3	1.02 (0.12)	-0.43 (0.25)	0.55 (0.75)	5	0.75 (0.71)	0.07 (0.40)	0.61 (1.56)	-0.05 (1.05)
Samos	*"Hipparion"* cf. *proboscideum*	3	-0.01 (0.38)	-0.23 (0.35)	0.90 (0.24)	4	-0.55 (0.93)	-0.38 (0.56)	-0.29 (0.98)	-0.54 (0.84)
Samos	*"Hippotherium"* cf. *brachypus*	1	-1.11	-0.42	1.41					
Samos	*"Hippotherium"* cf. *giganteum*					4	1.45 (0.39)	-0.43 (0.37)	-0.66 (1.46)	0.77 (0.72)
Samos	*Cremohipparion matthewi*					4	0.84 (0.72)	-0.35 (0.23)	0.44 (0.65)	-0.17 (0.93)
Samos	*Hipparion* cf. *dietrichi*	5	0.82 (0.61)	0.97 (0.49)	1.21 (1.43)	6	0.02 (0.71)	0.37 (1.60)	0.46 (1.33)	1.36 (1.33)
Samos	*Hipparion* sp. SONDAAR 1971	4	0.58 (0.76)	1.47 (0.83)	0.60 (0.62)	1	0.43	-0.02	0.67	0.15
Samos	*'Hipparion"* sp. (Quarry 6, Samos)	1	-1.21	0.60	1.56					
Ravin de la Pluie	*"Hipparion"* aff. *depereti*					1	-0.46	0.23	-0.49	-0.48
Ravin de la Pluie	*Cremohipparion macedonicum*					1	1.54	0.96	-0.65	-0.41
Ravin de la Pluie	*Hippotherium primigenium*					1	0.12	-0.51	-0.44	-0.61
Saloniki	*"Hipparion"* sp. 1 (Saloniki)	1	0.75	1.66	-1.08					
Saloniki	*"Hipparion"* spp. (Saloniki)	1	1.67	-0.96	-1.17	4	1.35 (1.02)	-0.93 (1.34)	0.34 (0.55)	-0.06 (0.64)
Maramena	*Cremohipparion* cf. *matthewi*					2	1.33 (0.15)	-0.94 (1.05)	-0.21 (0.06)	-0.96 (0.49)
Höwenegg	*Hippotherium primigenium*	14	-0.83 (0.36)	0.62 (0.48)	-0.20 (0.54)	20	-0.75 (0.51)	-0.55 (0.56)	0.34 (0.80)	-0.13 (0.75)
Eppelsheim	*Hippotherium primigenium*	1	-0.52	0.05	-0.44	1	0.18	-0.66	-2.54	0.16

Esselborn	*Hippotherium primigenium*					2	-0.83 (0.12)	-1.22 (0.23)	-0.49 (0.49)	0.82 (1.59)
Dorn-Dürkheim	*Hippotherium kammerschmitti*	1	-0.12	-0.46	0.13					
Dorn-Dürkheim	*Hippotherium primigenium*					2	-1.10 (0.39)	-1.77 (0.43)	-0.48 (0.78)	0.11 (2.03)
Charmoille	*Hippotherium* cf. *primigenium*	2	-1.19 (0.09)	1.07 (0.56)	0.31 (1.88)	3	-0.66 (0.47)	-0.27 (0.41)	0.23 (0.24)	-0.07 (0.57)
Inzersdorf	*"Hipparion"* sp. 1 (Vienna Basin)	4	-0.95 (0.50)	0.74 (1.40)	0.30 (2.21)	4	-1.66 (0.76)	3.15 (1.88)	-0.21 (0.99)	-0.86 (1.05)
Prottes	*"Hipparion"* sp. 1 (Vienna Basin)					1	0.14	-0.39	-1.32	-1.66
Gols	*"Hipparion"* sp. 2 (Vienna Basin)	1	-0.50	0.43	1.56					
Gols	*"Hipparion"* sp. 3 (Vienna Basin)	1	0.33	-0.10	0.68					
Schwechat	*"Hipparion"* sp. 1 (Vienna Basin)	1	-0.41	-0.04	0.59					
Sümeg	*Hippotherium sumegense*	1	-1.73	0.05	0.25					
Csákvár	*"Hippotherium"* cf. *brachypus*	2	-0.23 (0.88)	0.00 (0.30)	-0.90 (0.84)	2	-0.30 (0.06)	-1.47 (0.49)	0.98 (0.47)	0.48 (0.05)
Csákvár	*Hippotherium* cf. *intrans*	1	-0.29	2.19	-0.15					
Polgárdi	*"Hippotherium"* cf. *brachypus*	2	-0.45 (0.23)	-0.53 (0.20)	-0.80 (0.99)	2	-0.21 (0.20)	-1.09 (0.14)	-0.18 (0.75)	-0.14 (0.61)
Baltavár	*"Hippotherium"* cf. *brachypus*					1	-0.66	-0.75	0.28	0.24
Baltavár	*Hipparion microdon*	9	-0.75 (0.40)	0.11 (0.61)	-0.36 (0.53)	8	-0.21 (0.37)	-0.57 (0.52)	-0.53 (0.76)	-0.68 (0.64)
Kislang	*"Plesiohipparion" moritorum*					1	1.43	-0.93	-0.58	-1.05
Mont Luberon	*Hipparion prostylum*	4	0.34 (0.44)	-0.45 (0.54)	-0.77 (0.86)	7	0.85 (1.06)	-0.93 (1.13)	0.45 (0.63)	-0.65 (0.35)

Sinap	*"Hipparion" kecigibi*	5	-0.52 (0.87)	0.33 (1.07)	0.14 (0.69)	5	-1.00 (0.40)	0.41 (0.48)	-0.52 (1.10)	-0.75 (0.26)
Sinap	*"Hipparion"* sp. (Upper Sinap)	1	0.28	0.35	-0.54	1	1.50	-0.42	-0.45	-0.83
Sinap	*"Hipparion"* sp. 1 (Cursorial Morph)	2	-0.17 (0.42)	-1.67 (2.37)	-0.17 (1.49)	5	0.47 (0.77)	-0.10 (1.60)	0.00 (1.72)	-1.14 (0.91)
Sinap	*"Hipparion" uzunagizli*	1	1.28	0.24	1.65	2	0.69 (0.52)	-0.69 (1.05)	-1.58 (0.26)	-0.38 (0.49)
Sinap	*Cormohipparion sinapensis*	2	-0.31 (0.30)	0.86 (0.55)	-0.65 (0.77)	4	-0.18 (0.52)	-0.04 (0.73)	0.39 (0.22)	-0.46 (0.58)
Sinap	*indet. indet.*	2	0.67 (0.13)	1.67 (3.01)	-1.69 (0.79)					
Esme Akçaköy	*"Hipparion"* sp. (Esme Akçaköy)	4	0.37 (0.48)	-0.28 (1.12)	-0.96 (1.23)	7	-0.10 (0.50)	-0.68 (0.39)	-0.39 (0.56)	-0.14 (0.64)
Akkaşdağı	*"?Plesiohipparion"* cf. *longipes*	8	2.00 (0.30)	0.63 (0.46)	-0.08 (0.63)	12	0.99 (0.53)	1.01 (0.70)	0.82 (0.73)	0.72 (0.58)
Akkaşdağı	*"Hippotherium"* cf. *brachypus*	5	0.05 (0.43)	-0.25 (0.58)	-0.21 (1.16)	6	-0.30 (0.37)	0.52 (0.45)	-0.30 (0.47)	-0.08 (0.68)
Akkaşdağı	*Cremohipparion* cf. *moldavicum*	14	0.68 (0.45)	0.61 (1.02)	-0.57 (1.19)	15	0.27 (0.43)	0.85 (0.75)	0.61 (0.82)	0.36 (0.55)
Akkaşdağı	*Hipparion* cf. *dietrichi*	6	1.17 (0.35)	0.24 (1.46)	0.35 (0.62)	15	0.57 (0.45)	0.70 (0.61)	0.49 (1.02)	0.76 (0.98)
Çalta	*"?Plesiohipparion"* cf. *longipes*					1	2.12	0.41	2.31	0.24
Çalta	*Hipparion heintzi*	5	-1.12 (0.62)	-1.19 (0.45)	0.04 (0.37)	2	-1.29 (0.13)	0.58 (0.42)	-1.30 (0.39)	0.34 (1.33)
Siwaliks	*"Hipparion" antelopinum*	1	0.72	-0.34	0.46	4	0.39 (0.70)	-0.66 (0.89)	0.41 (0.77)	0.47 (0.36)
Siwaliks	*"Hipparion"* sp. (Siwaliks)					1	-0.29	-1.78	-0.59	2.54
Siwaliks	*"Sivalhippus"* cf. *perimense*					1	-1.31	-1.34	-0.46	-1.42
Siwaliks	*"Sivalhippus" perimense*	1	0.07	-0.28	-0.13	4	-1.73 (0.47)	0.16 (0.28)	-1.44 (1.26)	0.36 (1.00)

Molayan	*Hipparion molayanense*					5	0.39 (1.02)	0.95 (0.92)	1.18 (1.42)	0.40 (3.35)
Maragheh	*"Hipparion"* sp. (Maragheh)	2	-0.10 (0.05)	0.32 (0.37)	0.18 (0.57)					
Maragheh	*"Hippotherium"* cf. *brachypus*	2	-0.54 (0.76)	-0.12 (1.10)	-0.15 (1.08)	1	-0.68	0.88	-0.51	-0.66
Maragheh	*Cremohipparion* aff. *moldavicum*	10	1.32 (0.43)	-0.16 (0.98)	0.05 (0.52)	8	0.59 (0.64)	0.43 (0.64)	0.23 (0.52)	0.32 (1.07)
Maragheh	*Cremohipparion* cf. *matthewi*	4	0.47 (0.57)	-0.10 (0.65)	0.29 (1.49)	3	1.35 (0.62)	0.75 (0.50)	-0.87 (0.95)	-0.77 (0.91)
Maragheh	*Hipparion* cf. *prostylum*	7	0.32 (0.51)	0.08 (0.48)	-0.08 (0.76)	3	0.39 (0.09)	0.60 (0.62)	-0.63 (0.22)	-0.24 (1.03)
Kalmakpai	*Hipparion* cf. *elegans*					1	1.85	0.60	0.25	-0.45
Bou Hanifia	*"Hippotherium" africanum*					3	-0.44 (0.39)	2.28 (1.08)	-1.02 (0.73)	0.18 (1.25)
Sahabi	*"Cremohipparion"* aff. *matthewi*	1	-0.33	-2.10	-1.03					
Lothagam	*Eurygnatohippus feibeli*	1	1.55	-0.66	1.25					
Lothagam	*Eurygnatohippus turkanense*	1	-0.81	-0.29	-0.13	1	-0.21	-1.01	-1.45	-0.41
Christmas Quarry	*Cormohipparion occidentale* Medium	7	-1.02 (0.69)	-0.02 (0.93)	-0.49 (1.18)	20	-1.01 (0.48)	-0.13 (0.46)	0.14 (0.75)	0.35 (0.82)

Key: *N*, sample size; PC#, mean principal component score; (), standard deviation.

Table 6.6: Provisional classification of hipparionine metapodials from Samos.

Element	Specimen	Quarry	Morph	Species
MT III	AMNH23055B	Quarry 5	Samos Dwarf Elongate Morph	*Cremohipparion matthewi*
MT III	AMNH23055C	Quarry 5	Samos Dwarf Elongate Morph	*Cremohipparion matthewi*
MT III	AMNH23055D	Quarry 5	Samos Dwarf Elongate Morph	*Cremohipparion matthewi*
MT III	AMNH23055E	Quarry 5	Samos Dwarf Elongate Morph	*Cremohipparion matthewi*
MT III	AMNH23044	Quarry 1	Samos Large Morph	*"Hipparion"* cf. *proboscideum*
MT III	AMNH23044B	Quarry 1	Samos Large Morph	*"Hipparion"* cf. *proboscideum*
MT III	AMNH20764A	Quarry 4	Samos Large Morph	*"Hipparion"* cf. *proboscideum*
MT III	AMNH22841a		Samos Large Morph	*"Hipparion"* cf. *proboscideum*
MT III	AMNH23043E	Quarry 1	Samos Midsize Elongate Morph	*Hipparion* cf. *dietrichi*
MT III	AMNH20764x	Quarry 4	Samos Midsize Elongate Morph	*Hipparion* cf. *dietrichi*
MT III	AMNH20663		Samos Midsize Elongate Morph	*Hipparion* cf. *dietrichi*
MT III	AMNH20687A		Samos Midsize Elongate Morph	*Hipparion* cf. *dietrichi*
MT III	AMNH23066		Samos Midsize Elongate Morph	*Hipparion* cf. *dietrichi*
MT III	AMNHRLB0204		Samos Midsize Elongate Morph	*Hipparion* cf. *dietrichi*
MT III	AMNH22914	Quarry 5	Samos Small Elongate Morph	*Hipparion* sp. SONDAAR 1971
MT III	AMNHFM140295	Quarry 1	Samos Small Slender Morph	*"Hippotherium"* cf. *giganteum*
MT III	AMNH20764b	Quarry 4	Samos Small Slender Morph	*"Hippotherium"* cf. *giganteum*
MT III	AMNH20764e	Quarry 4	Samos Small Slender Morph	*"Hippotherium"* cf. *giganteum*
MT III	AMNH140925		Samos Small Slender Morph	*"Hippotherium"* cf. *giganteum*

MC III	AMNH23045	Quarry 1	Samos Large Morph	*"Hipparion"* cf. *proboscideum*
MC III	AMNH20674B	Quarry 4	Samos Large Morph	*"Hipparion"* cf. *proboscideum*
MC III	AMNH20764f	Quarry 4	Samos Large Morph	*"Hipparion"* cf. *proboscideum*
MC III	AMNH20764g	Quarry 4	Samos Midsize Elongate Morph	*Hipparion* cf. *dietrichi*
MC III	AMNH23102		Samos Midsize Elongate Morph	*Hipparion* cf. *dietrichi*
MC III	AMNH23059A	Quarry 5	Samos Midsize Elongate Morph	*Hipparion* sp. SONDAAR 1971
MC III	AMNH23059b	Quarry 5	Samos Midsize Elongate Morph	*Hipparion* sp. SONDAAR 1971
MC III	AMNH10737b		Samos Midsize Shortened Morph	*"Hippotherium"* cf. *brachypus*
MC III	AMNH23046b	Quarry 1	Samos Small Elongate Morph	*Hipparion* cf. *dietrichi*
MC III	AMNHRLB0201		Samos Small Elongate Morph	*Hipparion* cf. *dietrichi*
MC III	AMNHRLB0202		Samos Small Elongate Morph	*Hipparion* cf. *dietrichi*
MC III	AMNH22923	Quarry 5	Samos Small Elongate Morph	*Hipparion* sp. SONDAAR 1971
MC III	AMNH23052	Quarry 5	Samos Small Elongate Morph	*Hipparion* sp. SONDAAR 1971
MC III	AMNHFM140292	Quarry 6	Samos Small Shortened Morph	*"Hipparion"* sp. (Quarry 6, Samos)

Table 6.7: Mean values of $\log_{10}$(MGSV) by site and possible species.

		MC III			MT III		
Site	**Species**	***N***	**X**	**SD**	***N***	**X**	**SD**
Los Valles de Fuentidueña	Hipparion melendezi	1	1.45		4	1.48	0.0040
El Lugarejo	Hipparion melendezi	2	1.41	0.0002	1	1.46	
Santiga	"Hipparion" cf. depereti	4	1.43	0.0163	4	1.45	0.0098
Can Llobateres	"Hippotherium" aff. catalaunicum (Can Llobateres)	3	1.47	0.0050	3	1.48	0.0187
Can Llobateres	"Hippotherium" cf. catalaunicum	1	1.44				
Polinya	"Hippotherium" aff. catalaunicum	1	1.44				
La Tarumba	"Hippotherium" aff. catalaunicum	1	1.48				
Piera	"Hippotherium" aff. catalaunicum (Piera)	6	1.44	0.0089	2	1.48	0.0296
La Roma 2	"Hipparion" sp. (La Roma 2)	7	1.51	0.0090	16	1.55	0.0177
Concud	Hipparion concudense	7	1.44	0.0175	6	1.47	0.0151
La Gloria 4	Hipparion cf. elegans				1	1.47	
Ballestar	"Hippotherium" aff. catalaunicum				1	1.48	
Venta del Moro	Hipparion sp. (Venta del Moro)	2	1.39	0.0069	1	1.44	
Layna	Hipparion fissurae				1	1.49	
Pikermi	"Hippotherium" brachypus	2	1.47	0.0162	6	1.53	0.0150
Pikermi	Cremohipparion mediterraneum	3	1.42	0.0080	5	1.45	0.0150
Samos	"Hipparion" cf. proboscideum	3	1.53	0.0104	4	1.56	0.0155
Samos	"Hippotherium" cf. brachypus	1	1.45				
Samos	"Hippotherium" cf. giganteum				4	1.47	0.0060
Samos	Cremohipparion matthewi				4	1.38	0.0291
Samos	Hipparion cf. dietrichi	5	1.45	0.0274	6	1.50	0.0272
Samos	Hipparion sp. Sondaar 1971	4	1.45	0.0195	1	1.48	
Samos	'Hipparion" sp. (Quarry 6, Samos)	1	1.41				
Ravin de la Pluie	"Hipparion" aff. depereti				1	1.45	
Ravin de la Pluie	Cremohipparion macedonicum				1	1.38	
Ravin de la Pluie	Hippotherium primigenium				1	1.49	

Saloniki	"Hipparion" sp. 1 (Saloniki)	1	1.46				
Saloniki	"Hipparion" spp. (Saloniki)	1	1.43		4	1.44	0.0471
Maramena	Cremohipparion cf. matthewi				2	1.41	0.0011
Höwenegg	Hippotherium primigenium	14	1.48	0.0114	20	1.51	0.0146
Eppelsheim	Hippotherium primigenium	1	1.48		1	1.49	
Esselborn	Hippotherium primigenium				2	1.51	0.0024
Dorn-Dürkheim	Hippotherium kammerschmitti	1	1.45				
Dorn-Dürkheim	Hippotherium primigenium				2	1.53	0.0109
Charmoille	Hippotherium cf. primigenium	2	1.45	0.0194	3	1.49	0.0141
Inzersdorf	"Hipparion" sp. 1 (Vienna Basin)	4	1.45	0.0152	4	1.47	0.0122
Prottes	"Hipparion" sp. 1 (Vienna Basin)				1	1.48	
Gols	"Hipparion" sp. 2 (Vienna Basin)	1	1.44				
Gols	"Hipparion" sp. 3 (Vienna Basin)	1	1.48				
Schwechat	"Hipparion" sp. 1 (Vienna Basin)	1	1.44				
Sümeg	Hippotherium sumegense	1	1.45				
Csákvár	"Hippotherium" cf. brachypus	2	1.47	0.0176	2	1.53	0.0288
Csákvár	Hippotherium cf. intrans	1	1.45				
Polgárdi	"Hippotherium" cf. brachypus	2	1.47	0.0177	2	1.52	0.0031
Baltavár	"Hippotherium" cf. brachypus				1	1.53	
Baltavár	Hipparion microdon	9	1.43	0.0183	8	1.46	0.0141
Kislang	"Plesiohipparion" moritorum				1	1.57	
Mont Luberon	Hipparion prostylum	4	1.41	0.0094	7	1.44	0.0226
Sinap	"Hipparion" kecigibi	5	1.44	0.0170	5	1.48	0.0144
Sinap	"Hipparion" sp. (Upper Sinap)	1	1.46		1	1.41	
Sinap	"Hipparion" sp. 1 (Cursorial Morph)	2	1.44	0.0331	5	1.48	0.0096
Sinap	"Hipparion" uzunagizli	1	1.43		2	1.44	0.0022
Sinap	Cormohipparion sinapensis	2	1.44	0.0116	4	1.48	0.0080
Sinap	indet. indet.	2	1.47	0.0125			
Esme Akçaköy	"Hipparion" sp. (Esme Akçaköy)	4	1.47	0.0110	7	1.49	0.0139
Akkaşdağı	"?Plesiohipparion" cf. longipes	8	1.48	0.0080	12	1.52	0.0116
Akkaşdağı	"Hippotherium" cf. brachypus	5	1.53	0.0054	6	1.55	0.0110
Akkaşdağı	Cremohipparion cf. moldavicum	14	1.41	0.0174	15	1.44	0.0173
Akkaşdağı	Hipparion cf. dietrichi	6	1.48	0.0053	15	1.50	0.0145
Çalta	"?Plesiohipparion" cf. longipes				1	1.51	

Çalta	Hipparion heintzi	5	1.54	0.0150	2	1.57	0.0001
Siwaliks	"Hipparion" antelopinum	1	1.47		4	1.49	0.0210
Siwaliks	"Hipparion" sp. (Siwaliks)				1	1.58	
Siwaliks	"Sivalhippus" cf. perimense				1	1.61	
Siwaliks	"Sivalhippus" perimense	1	1.53		4	1.55	0.0163
Molayan	Hipparion molayanense				5	1.46	0.0297
Maragheh	"Hipparion" sp. (Maragheh)	2	1.39	0.0071			
Maragheh	"Hippotherium" cf. brachypus	2	1.49	0.0118	1	1.53	
Maragheh	Cremohipparion aff. moldavicum	10	1.45	0.0201	8	1.50	0.0254
Maragheh	Cremohipparion cf. matthewi	4	1.35	0.0053	3	1.40	0.0177
Maragheh	Hipparion cf. prostylum	7	1.40	0.0191	3	1.44	0.0081
Kalmakpai	Hipparion cf. elegans				1	1.48	
Bou Hanifia	"Hippotherium" africanum				3	1.46	0.0024
Sahabi	"Cremohipparion" aff. matthewi	1	1.38				
Lothagam	Eurygnatohippus feibeli	1	1.46				
Lothagam	Eurygnatohippus turkanense	1	1.55		1	1.60	
Christmas Quarry	Cormohipparion occidentale Medium	7	1.47	0.0080	20	1.48	0.0118

Key: *N*, sample size; X, mean habitat score; SD, standard deviation.

Table 6.8: Faunal list for La Roma 2.

Species	Source	Diet	Locomotion	Molar crown height
Insectivora				
Erinaceidae				
Galerix (Parasorex)	Alcala, 1994			
Talpidae				
Desmanella sp.	Alcala, 1994; NOW mammal database, n.d.	.	.	.
Rodentia				
Cricetidae				
Hispanomys sp.	Alcala, 1994; NOW mammal database, n.d.	.	.	.
Muridae				
Progonomys cf. *cathalai*	Alcala, 1994; NOW mammal database, n.d.	.	.	.
Lagomorpha				
Ochotonidae				
Prolagus crusafonti	Alcala, 1994; NOW mammal database, n.d.	.	.	.
Carnivora				
Felidae				
Felidae sp.	NOW mammal database, n.d	carnivore (meat)	.	.
Hyaenidae				
Lycyaena chaeretis	Alcala, 1994; NOW mammal database, n.d.	carnivore (meat/bone)	cursorial	.
Ictitheriinae indet.	Alcala, 1994; NOW mammal database, n.d.	.	.	.
Artiodactyla				
Suidae				
Microstonyx major	Alcala, 1994; NOW mammal database, n.d.	omnivore (predominantly plants)	general quadruped	brachydont

Bovidae				
Tragoportax gaudryi	Alcala, 1994; NOW mammal database, n.d.	browser	.	brachydont
Aragoral mudejar	Alcala, 1997; Alcala, 1994; NOW mammal database, n.d.	.	.	.
Protoryx sp.	NOW mammal database, n.d	mixed feeder	.	brachydont
Bovidae sp.	NOW mammal database, n.d	.	.	hypsodont
Moschidae				
Micromeryx flourensianus	NOW mammal database, n.d.; Alcala, 1994	browser	.	brachydont
Perissodactyla				
Equidae				
Hippotherium sp.	this work; Alcala, 1994; NOW mammal database, n.d.	mixed feeder	cursorial	hypsodont
Rhinocerotidae				
Aceratherium incisivum	Alcala, 1994; NOW mammal database, n.d.	browser	general quadruped	brachydont
Alicornops alfambrensis	Alcala, 1994; NOW mammal database, n.d.	browser	cursorial	mesodont
Dihoplus schleiermacheri	Alcala, 1994; NOW mammal database, n.d.	browser	general quadruped	mesodont
Proboscidea				
Gomphotheriidae				
Tetralophodon longirostris	NOW mammal database, n.d.; Alcala, 1994	mixed feeder	graviportal	brachydont

Table 6.9: Variation of possible conspecifics from different sites.

		MC III				MT III				
Species	**Sites**	***N***	**SD of siM1**	**SD of siM3**	**CV of MGSV**	***N***	**SD of siM1**	**SD of siM3**	**CV of MGSV**	**Single Species?**
"Hipparion" sp. (La Roma 2)	La Roma 2	7	0.0096	**0.0110**	0.0060	16	0.0098	0.0124	**0.0114**	standard
Hippotherium primigenium	Höwenegg	14	**0.0099**	0.0106	**0.0077**	20	**0.0128**	**0.0198**	0.0096	standard
"?Plesiohipparion" cf. *longipes*	Akkaşdağı, Çalta	8	0.0042	0.0135	0.0054	13	0.0198	0.0211	0.0077	plausible single species
"Hipparion" sp. 1 (Vienna Basin)	Inzersdorf, Prottes, Schwechat	5	0.0083	0.0162	0.0103	5	0.0067	0.0285	0.0084	plausible single species
"Hippotherium" cf. *brachypus*	Akkaşdağı, Baltavár, Csákvár, Maragheh, Pikermi, Polgárdi, Samos	14	0.0115	0.0196	0.0209	18	0.0147	0.0183	0.0106	plausible single species
Hipparion cf. *dietrichi*	Akkaşdağı, Samos	11	0.0119	0.0164	0.0156	21	0.0137	0.0212	0.0122	probably multiple species
Hipparion cf. *prostylum*	Mont Luberon, Maragheh	11	0.0070	0.0139	0.0115	10	0.0184	0.0166	0.0131	probably multiple species
Hippotherium cf. *primigenium*	Höwenegg, Dorn-Dürkheim, Eppelsheim, Esselborn, Charmoille, Ravin de la Pluie	17	0.0090	0.0145	0.0106	29	0.0139	0.0207	0.0102	probably multiple species
Hipparion cf. *melendezi*	El Lugarejo, Los Valles de Fuentidueña					5	0.0098	0.0062	0.0064	plausible single species
"Hippotherium" cf. *catalaunicum*	Can Llobateres, La Tarumba, Polinya	6	0.0110	0.0103	0.0115					
Cremohipparion cf. *matthewi*	Samos, Maragheh, Saloniki, Maramena					10	0.0116	0.0261	0.0158	

Key: *N*, sample size; SD, standard deviation; CV, coefficient of variation.

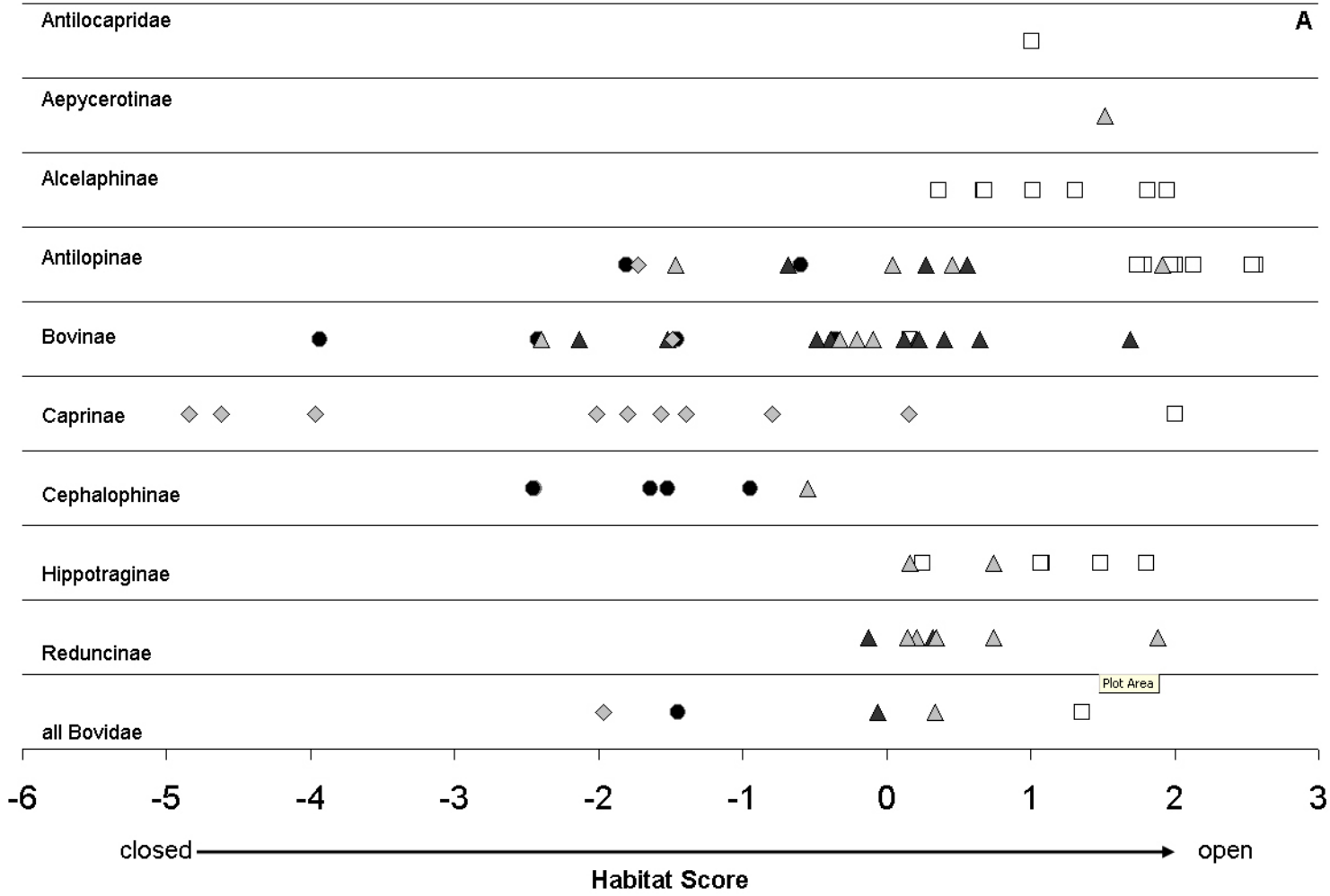
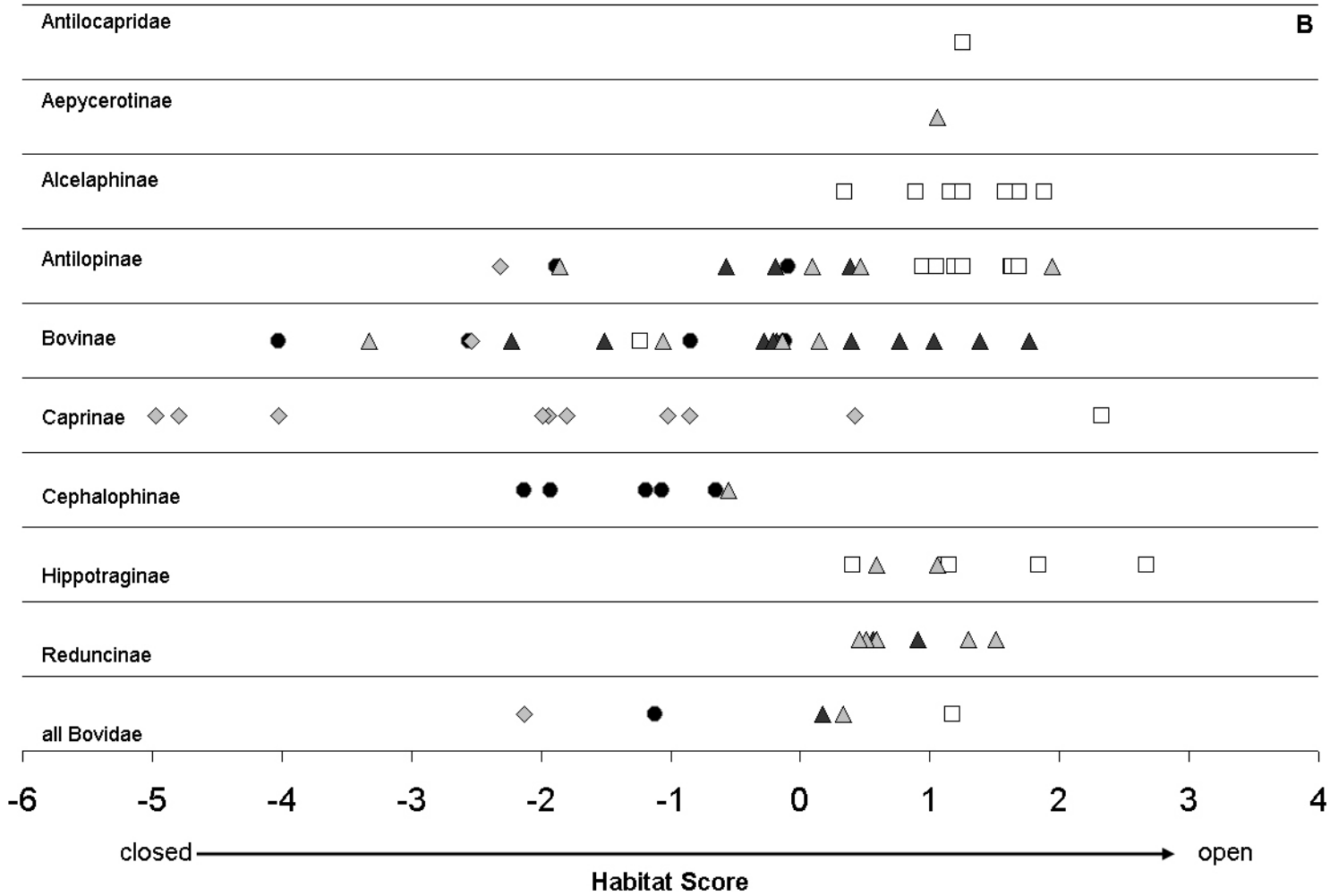


FIGURE 6.1: SUMMARY OF HABITAT SCORES FOR BOVIDS BY SUBFAMILY AND HABITAT CATEGORY. A, metatarsals; B, metacarpals. The horizontal axis is habitat score (based on size, metapodial length, and metapodial width at midshaft) and the vertical axis divides bovids by subfamily. The symbols further represent species according to habitat category. Closed circles (●) are forest species, dark triangles (▲) are heavy cover species, light triangles (▲) are light cover species, open squares (□) are plains dwellers, and light diamonds (◆)are mountain habitat forms. Mean habitat scores for all specimens in each habitat category are shown in the row corresponding to all Bovidae.



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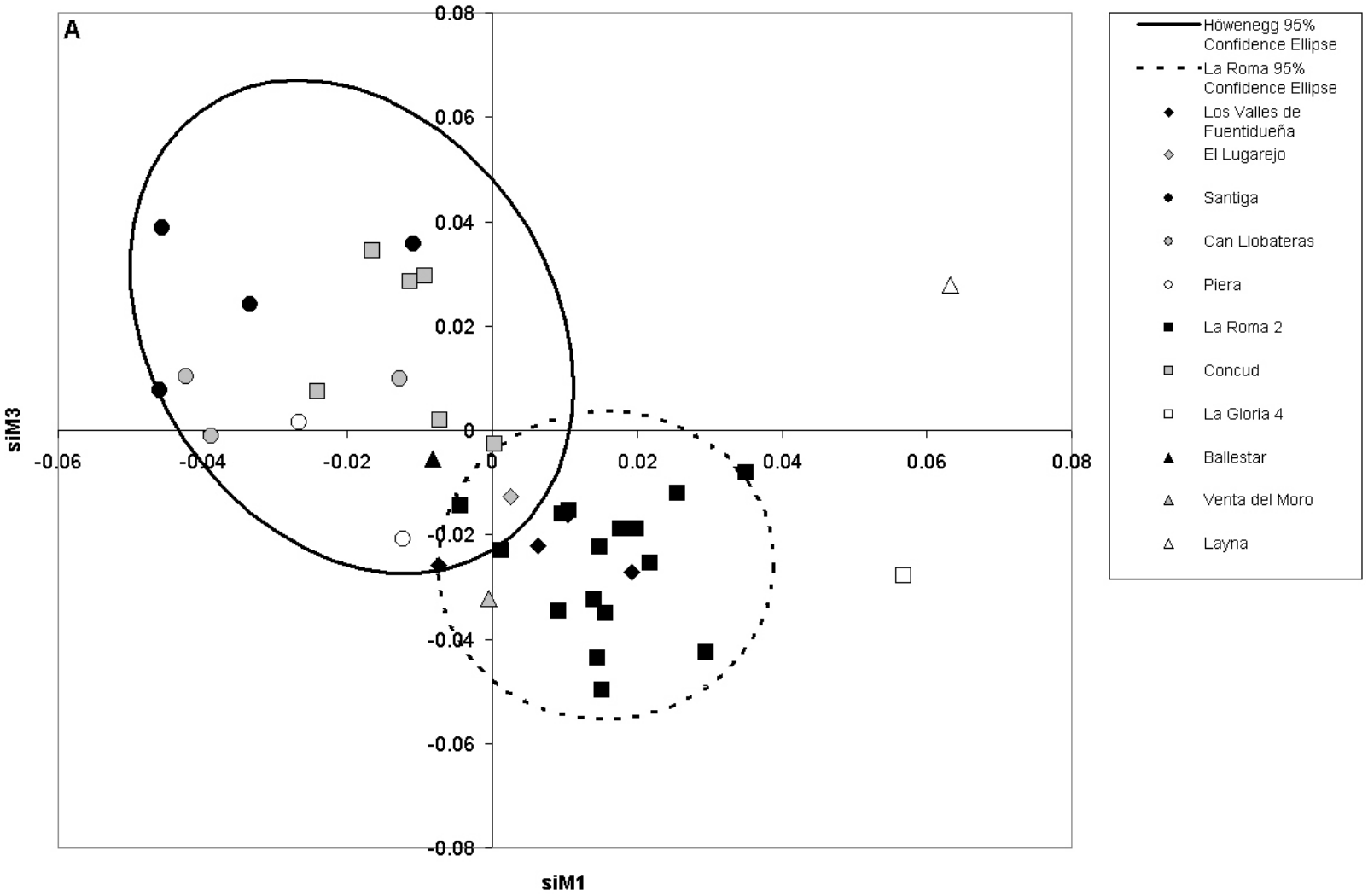
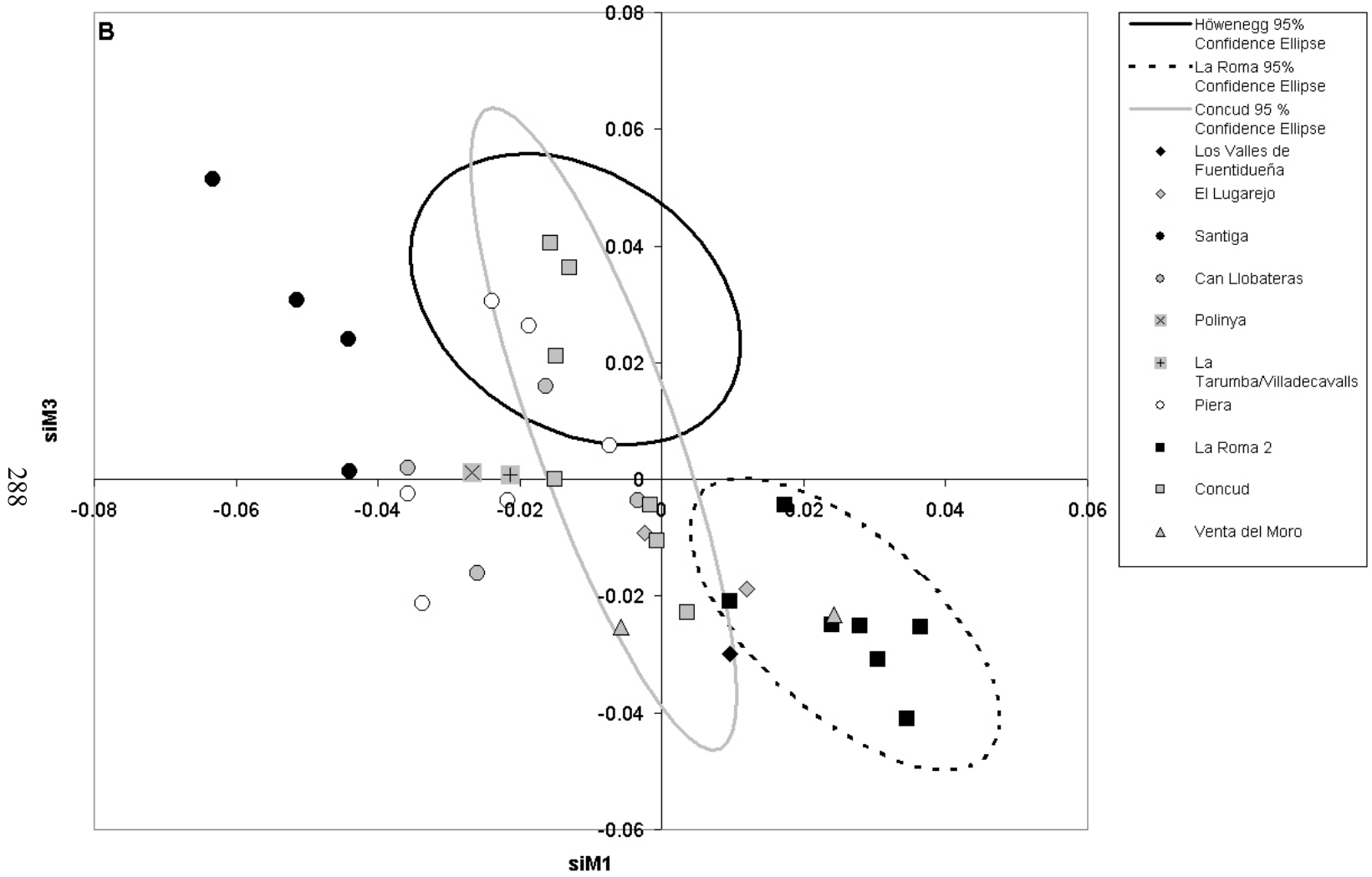


FIGURE 6.2: PLOT OF SIM3 AND SIM1 FOR HIPPARIONINES FROM SPAIN. A, MT III's; B, MC III's. Specimens are shown by site with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.



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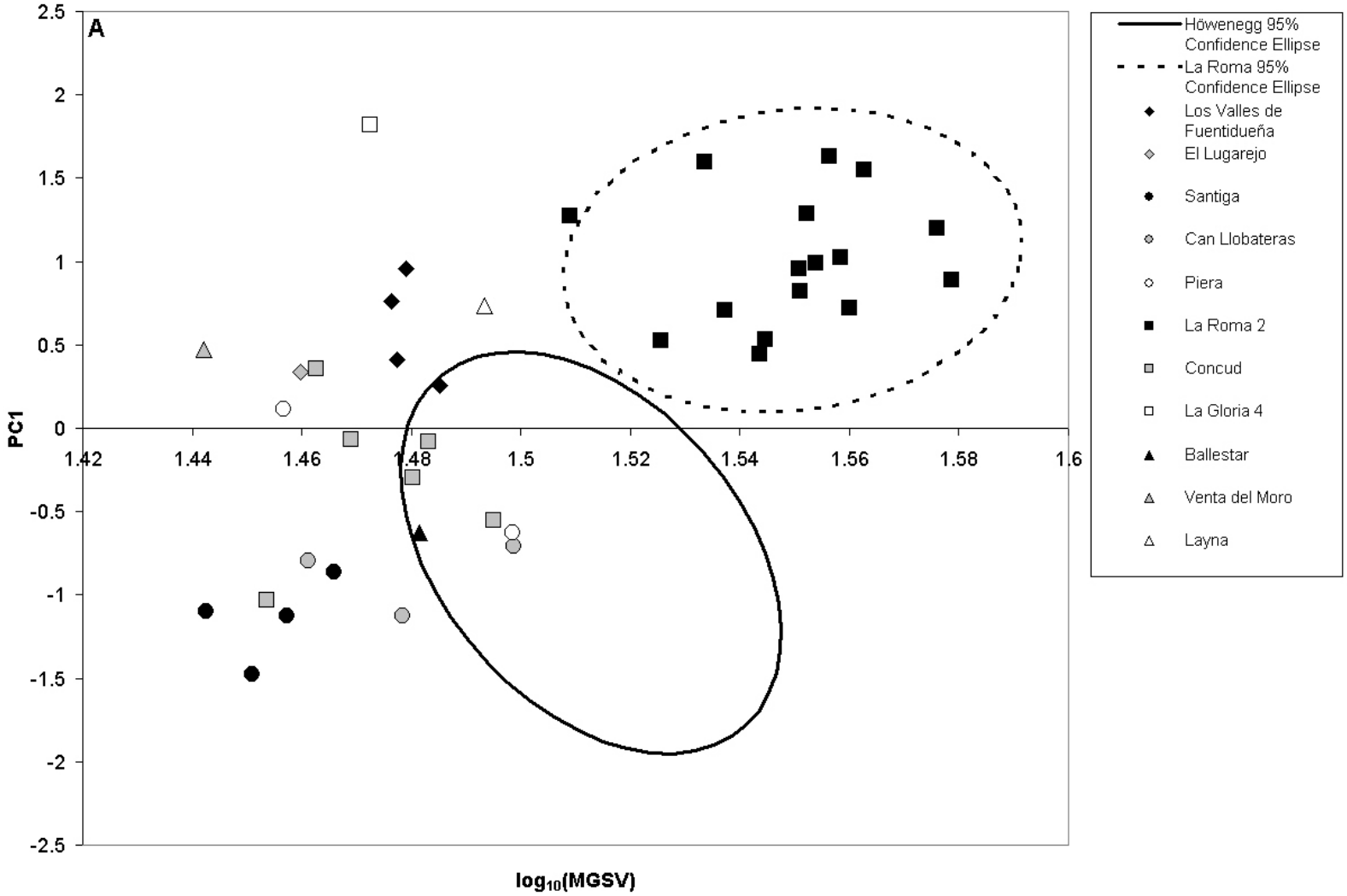


FIGURE 6.3: PLOT OF PC1 AND LOG10(MGSV) FOR HIPPARIONINES FROM SPAIN. A, MT III's; B, MC III's. Specimens are shown by site with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

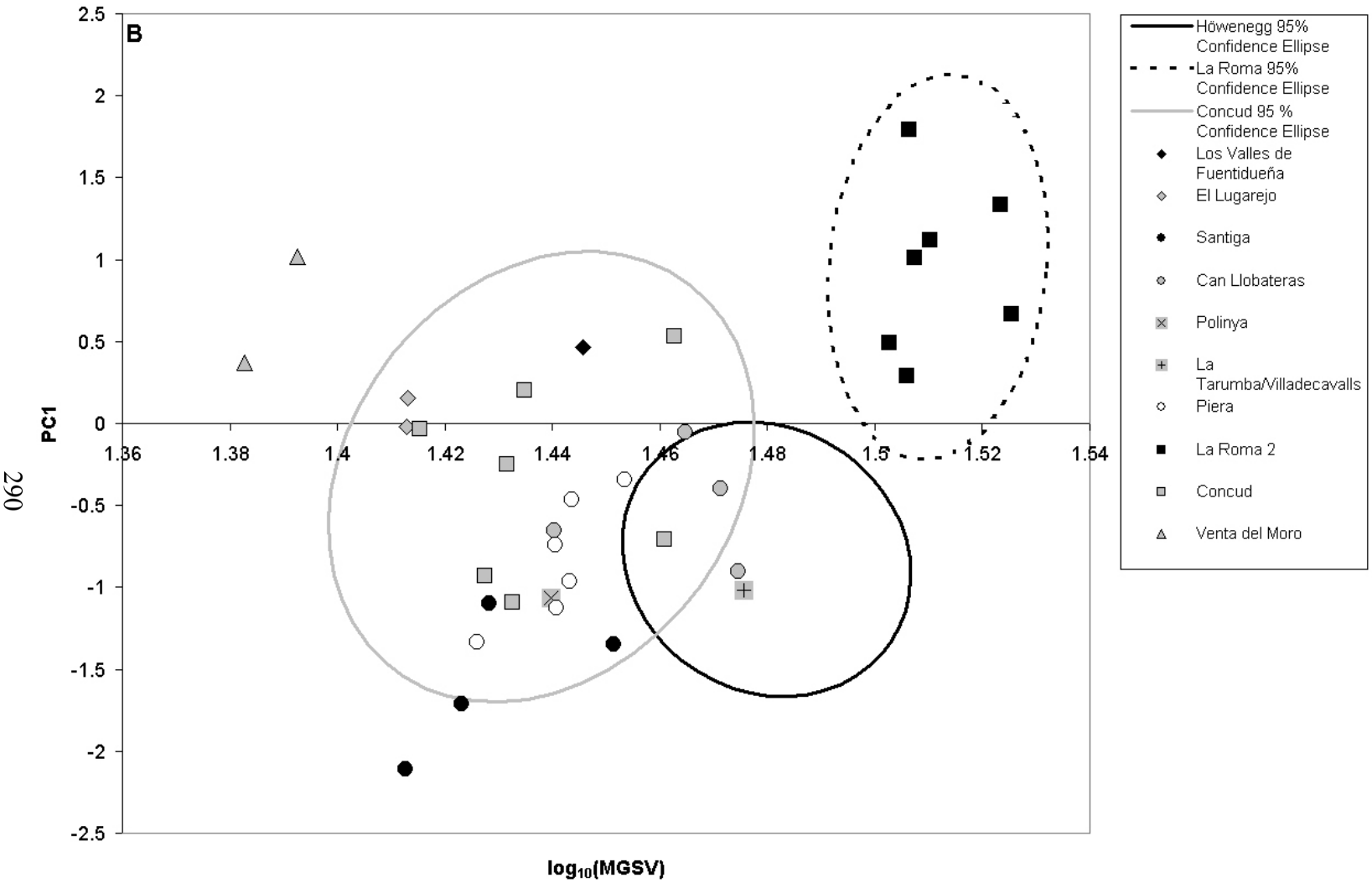


FIGURE 6.3: PLOT OF PC1 AND LOG10(MGSV) FOR HIPPARIONINES FROM SPAIN. A, MT III's; B, MC III's. Specimens are shown by site with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

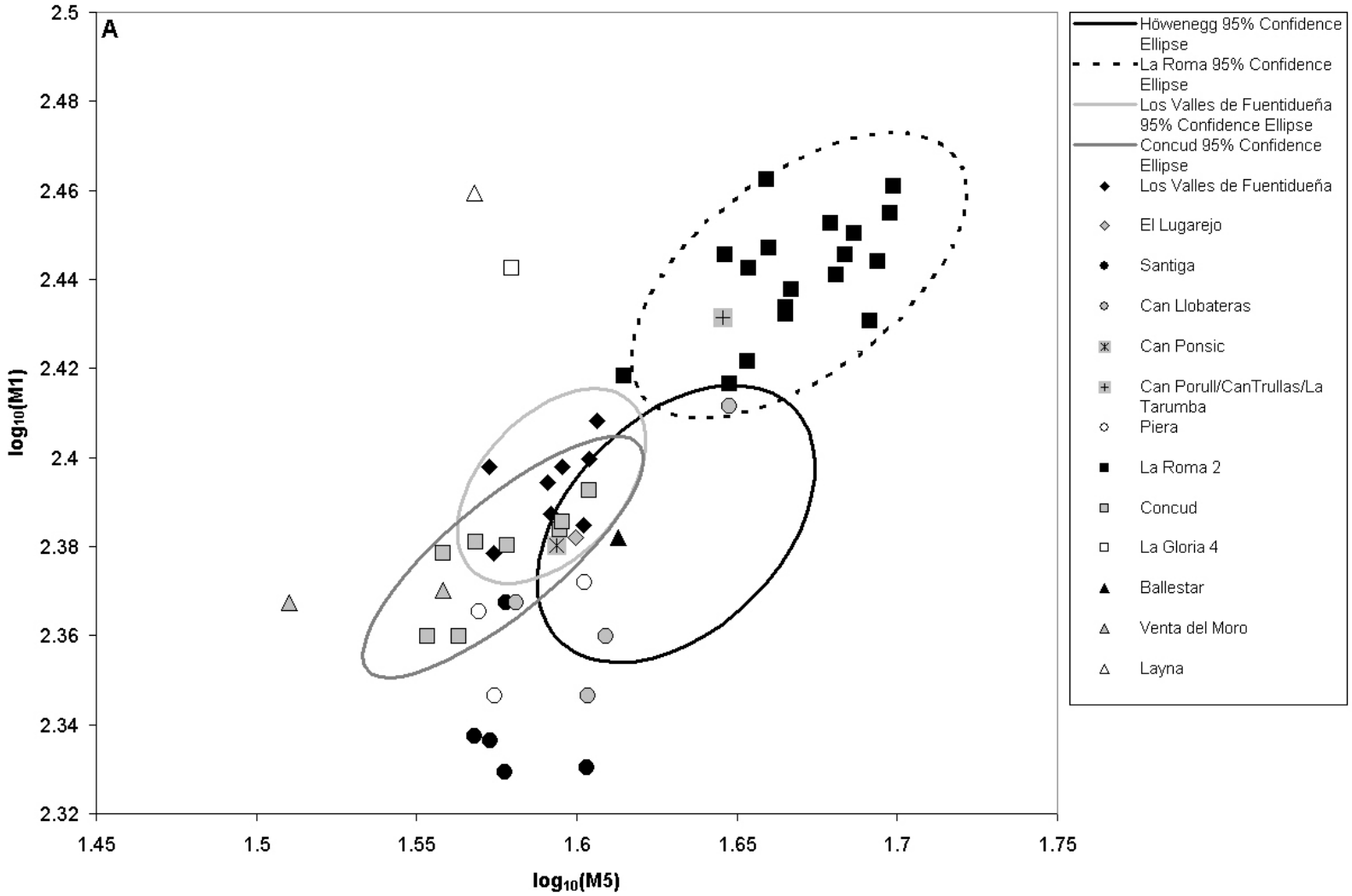


FIGURE 6.4: PLOT OF LOG10(M1) AND LOG10(M5) FOR HIPPARIONINES FROM SPAIN. A, MT III's; B, MC III's. Specimens are shown by site with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

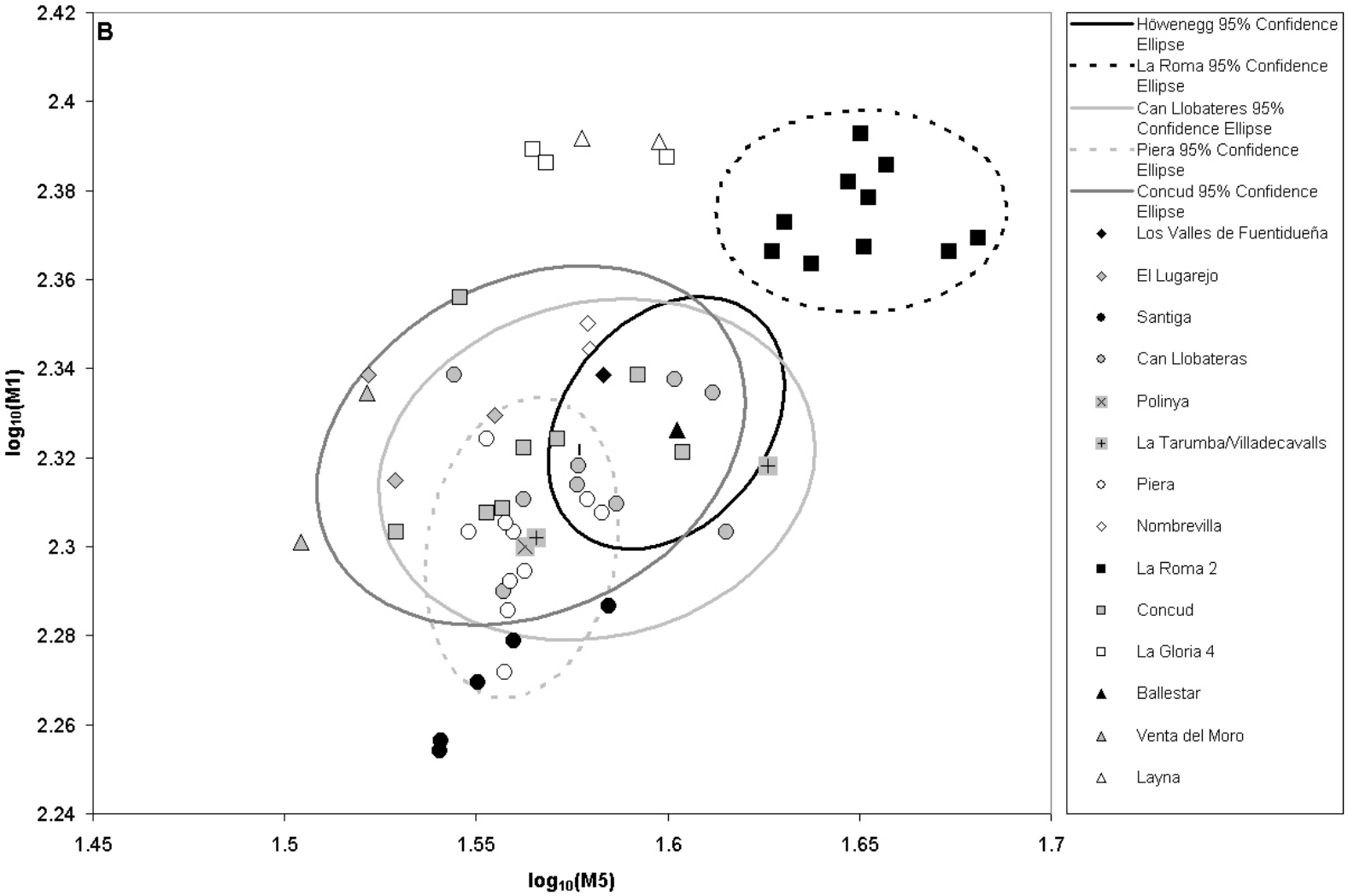


FIGURE 6.4: PLOT OF LOG10(M1) AND LOG10(M5) FOR HIPPARIONINES FROM SPAIN. A, MT III's; B, MC III's. Specimens are shown by site with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

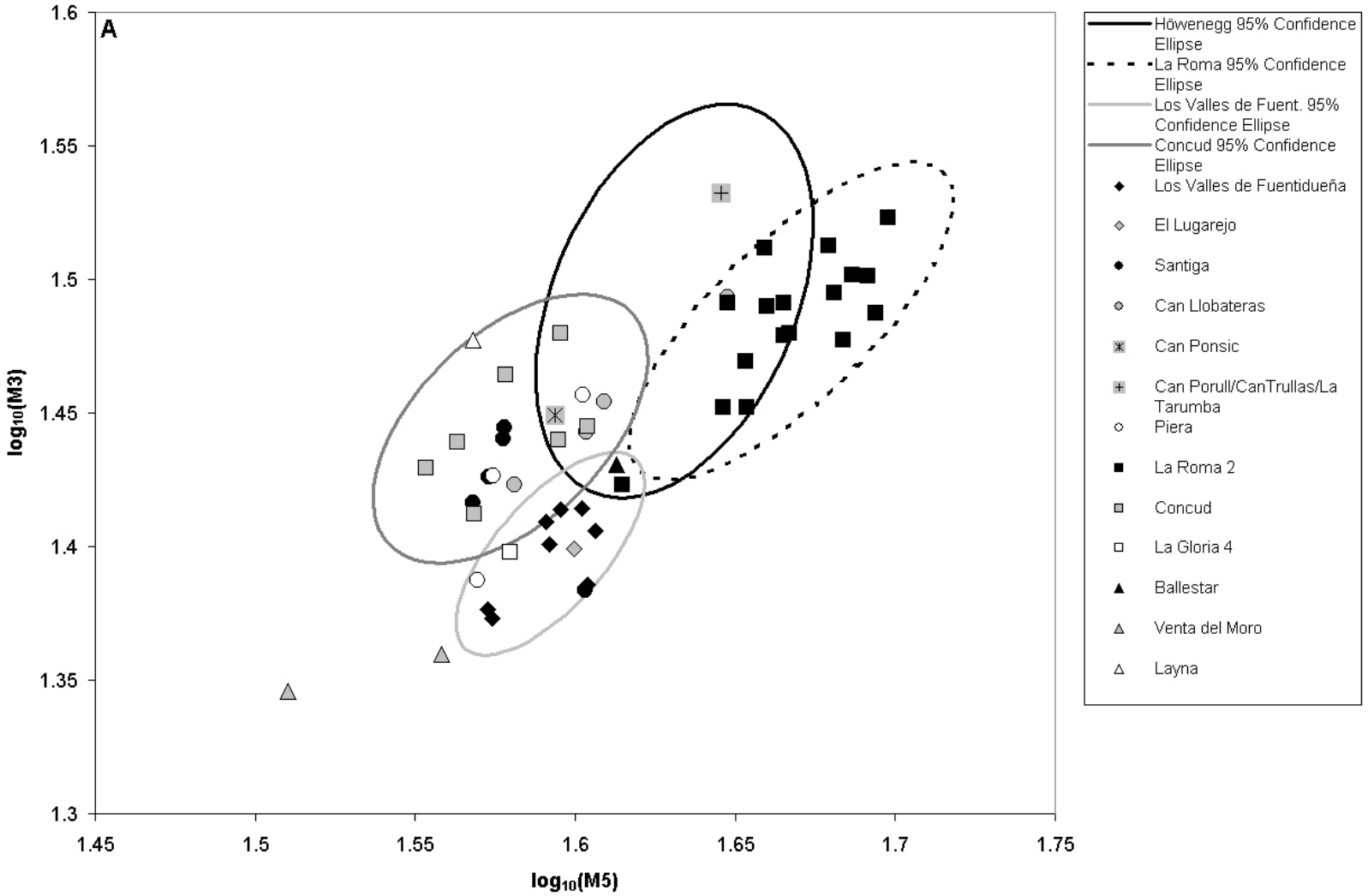


FIGURE 6.5: PLOT OF LOG10(M3) AND LOG10(M5) FOR HIPPARIONINES FROM SPAIN. A, MT III's; B, MC III's. Specimens are shown by site with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

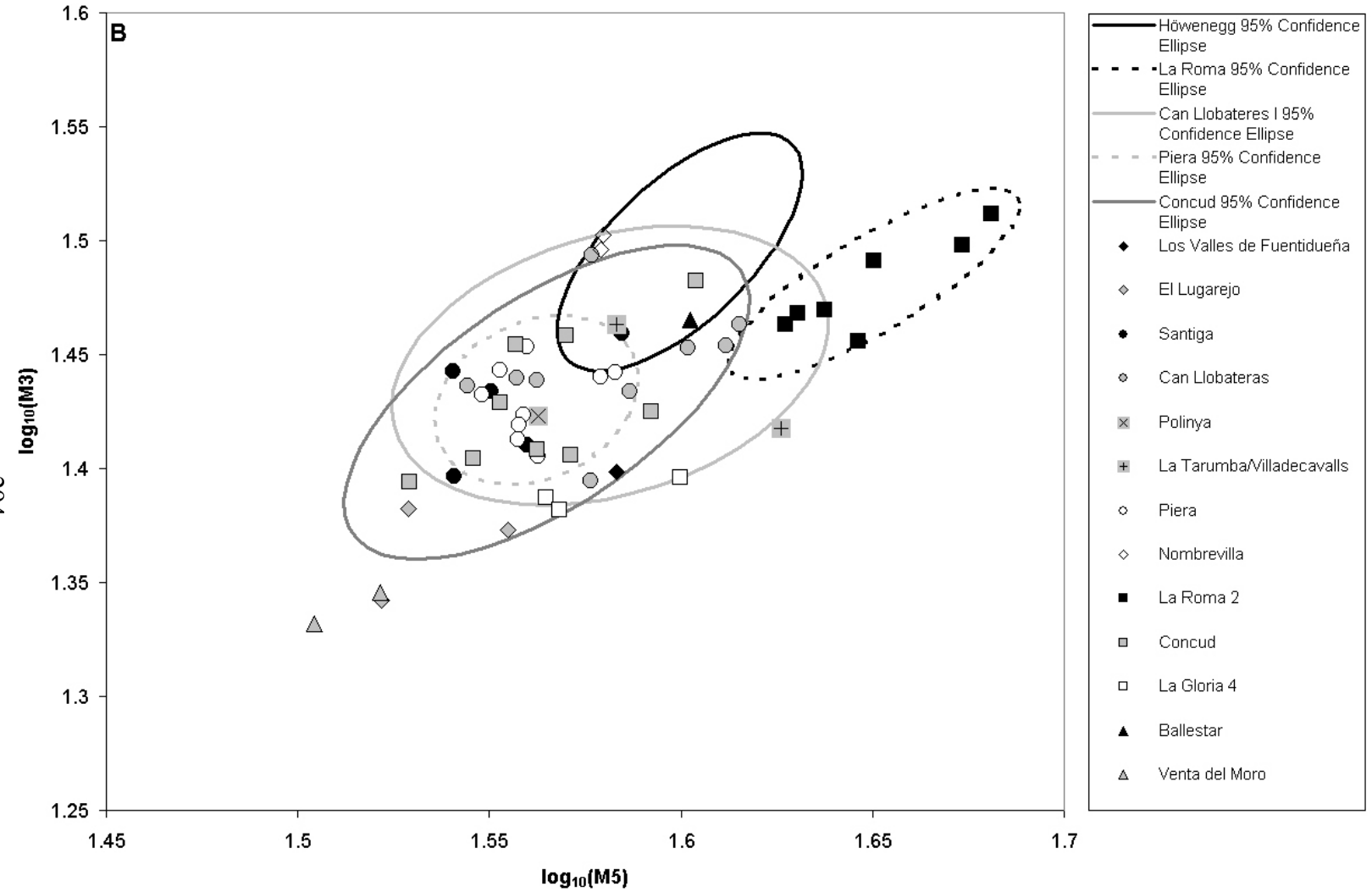


FIGURE 6.5: PLOT OF LOG10(M3) AND LOG10(M5) FOR HIPPARIONINES FROM SPAIN. A, MT III's; B, MC III's. Specimens are shown by site with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

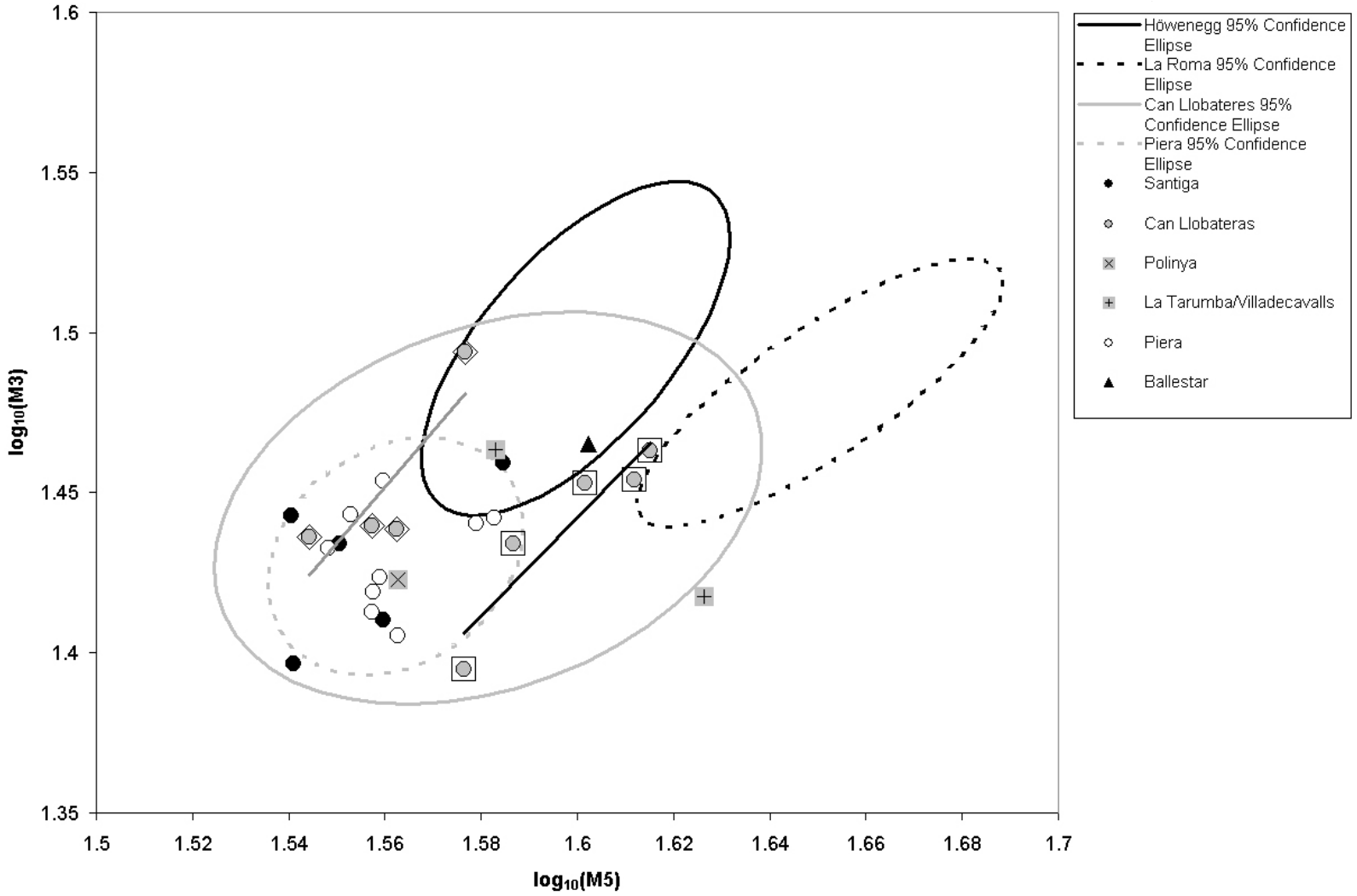


FIGURE 6.6: PLOT OF LOG10(M3) AND LOG10(M5) FOR SELECTED MC III'S FROM SPAIN. MC III'S FROM CAN Llobateres are divided into two possible species with separate best fit least squares regression lines.

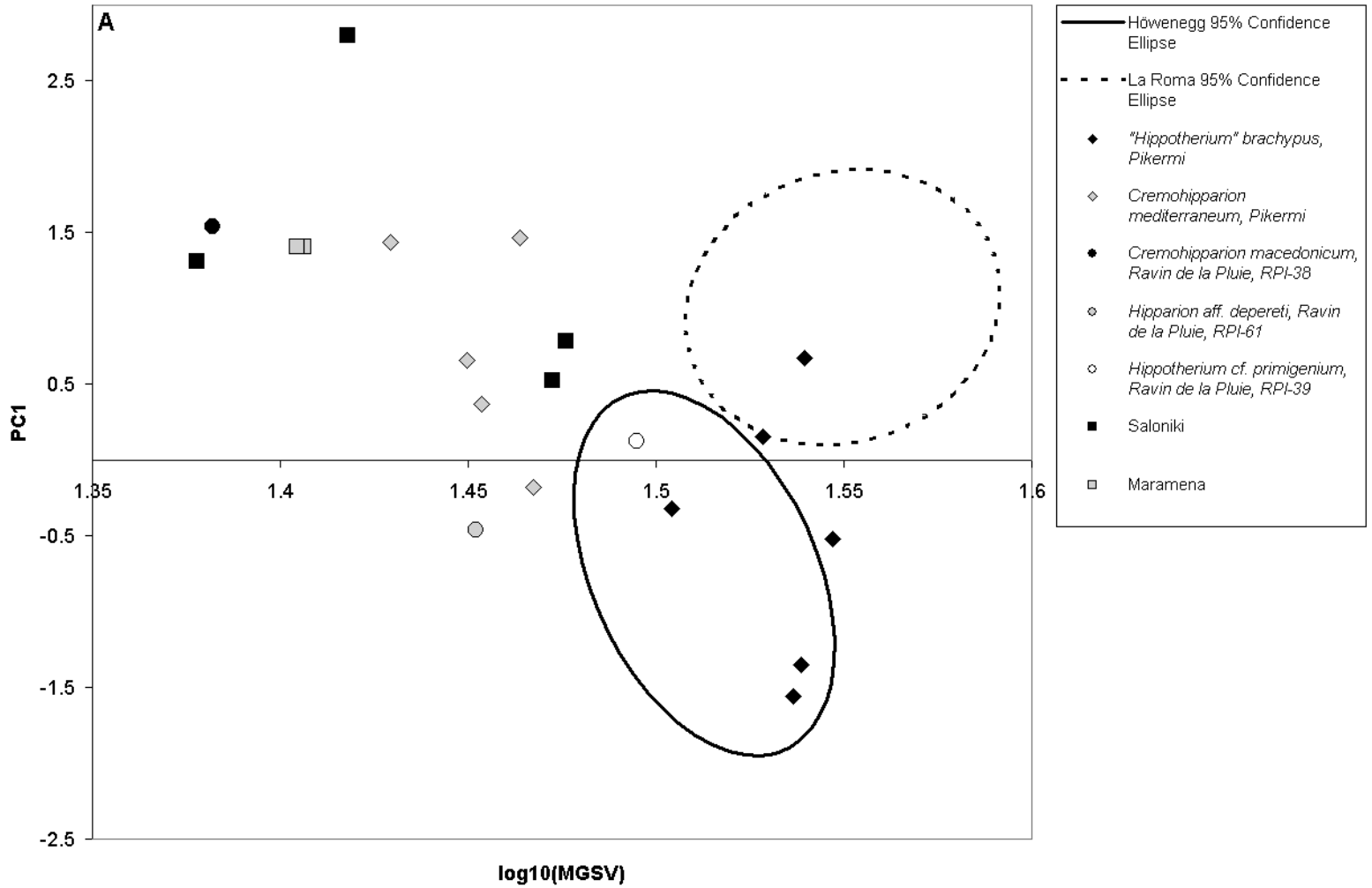


FIGURE 6.7: PLOT OF PC1 AND LOG10(MGSV) FOR HIPPARIONINES FROM PIKERMI, RAVIN DE LA PLUIE, SALONIKI, AND MARAMENA. A, MT III's; B, MC III's. Specimens are shown by site and/or possible taxonomic identification with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

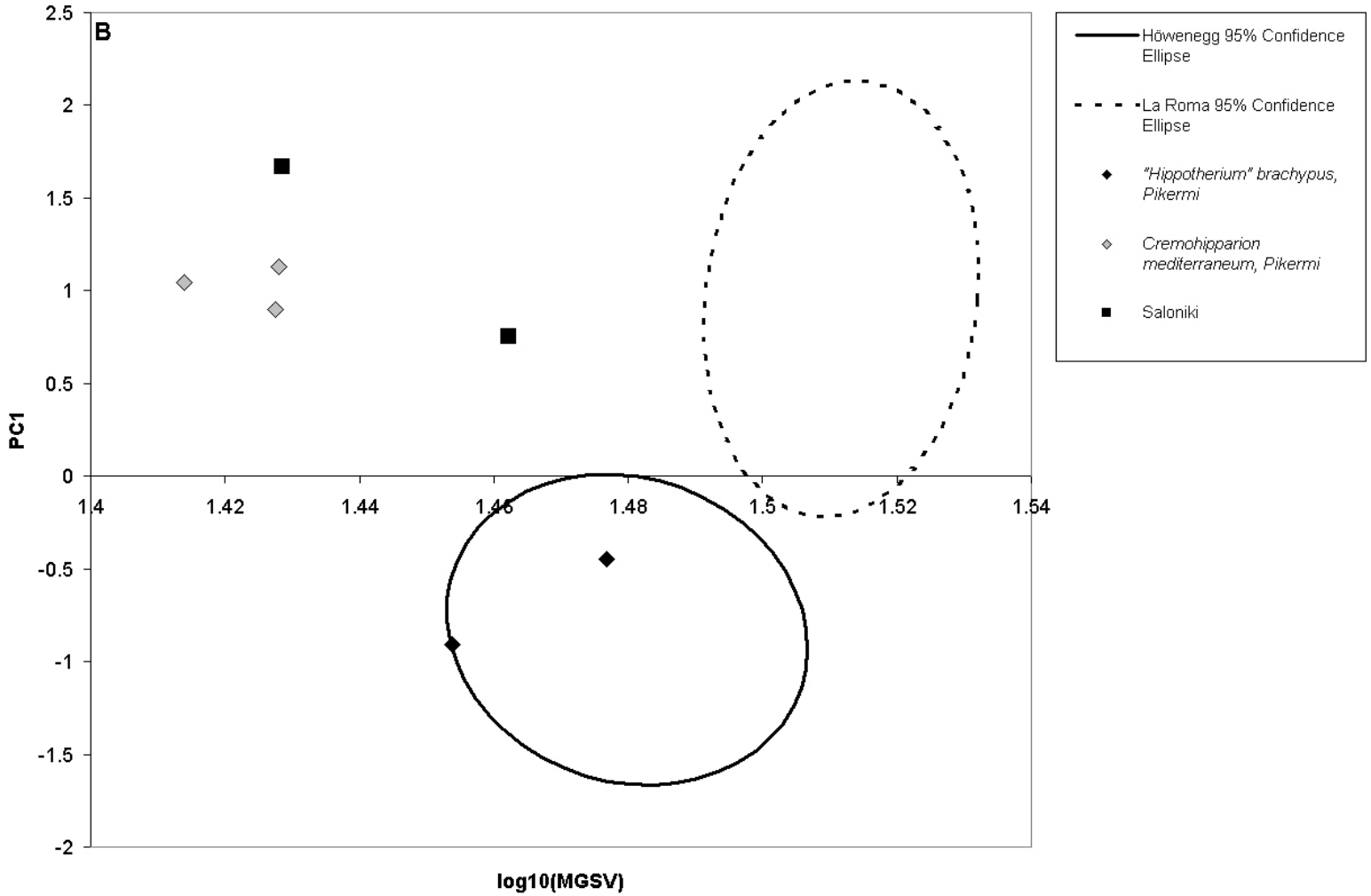


FIGURE 6.7: PLOT OF PC1 AND LOG10(MGSV) FOR HIPPARIONINES FROM PIKERMI, RAVIN DE LA PLUIE, SALONIKI, AND MARAMENA. A, MT III's; B, MC III's. Specimens are shown by site and/or possible taxonomic identification with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

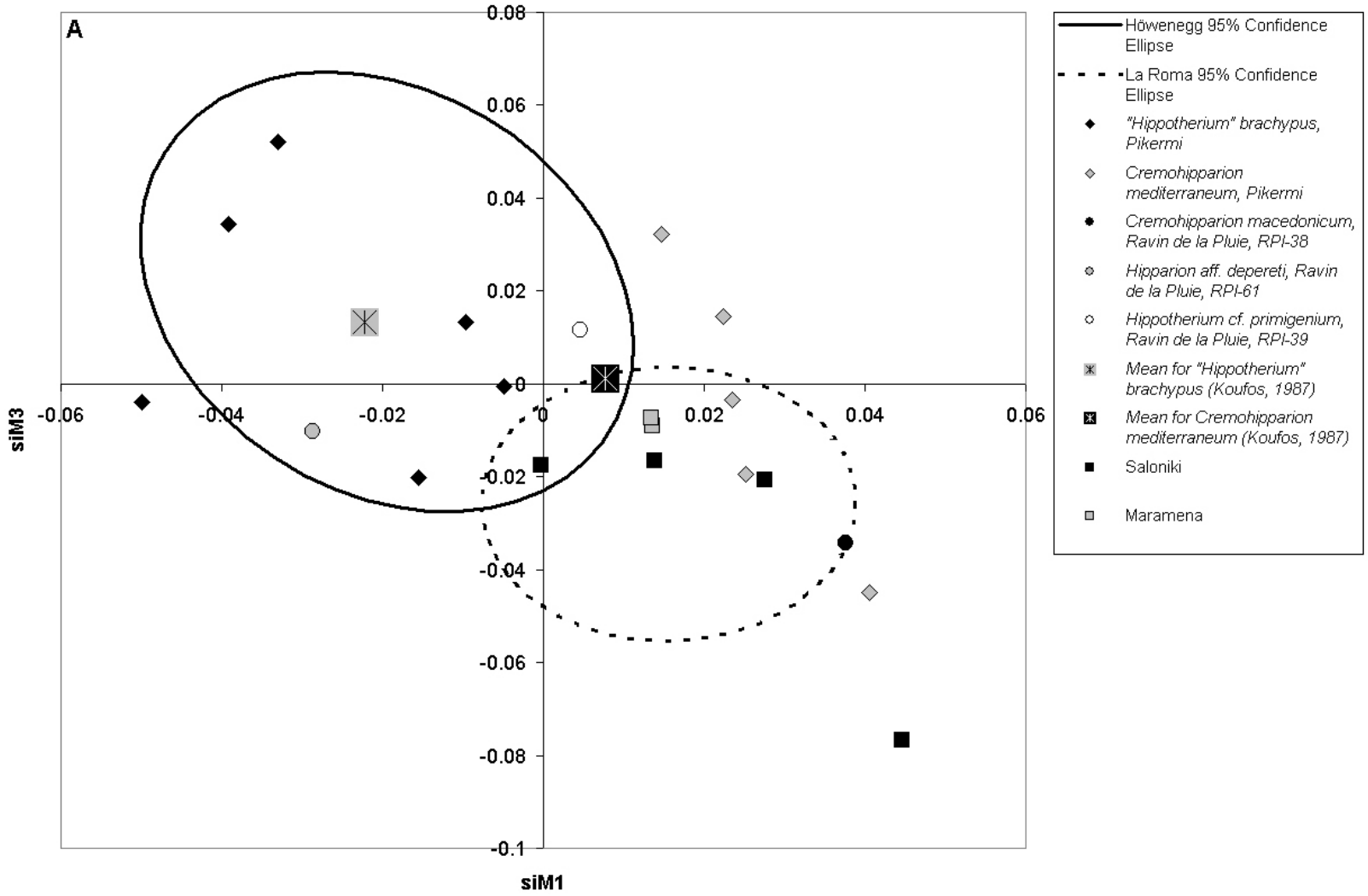


FIGURE 6.8: PLOT OF SIM3 AND SIM1 FOR HIPPARIONINES FROM PIKERMI, RAVIN DE LA PLUIE, SALONIKI, AND MARAMENA. A, MT III's; B, MC III's. Specimens are shown by site and/or possible taxonomic identification with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

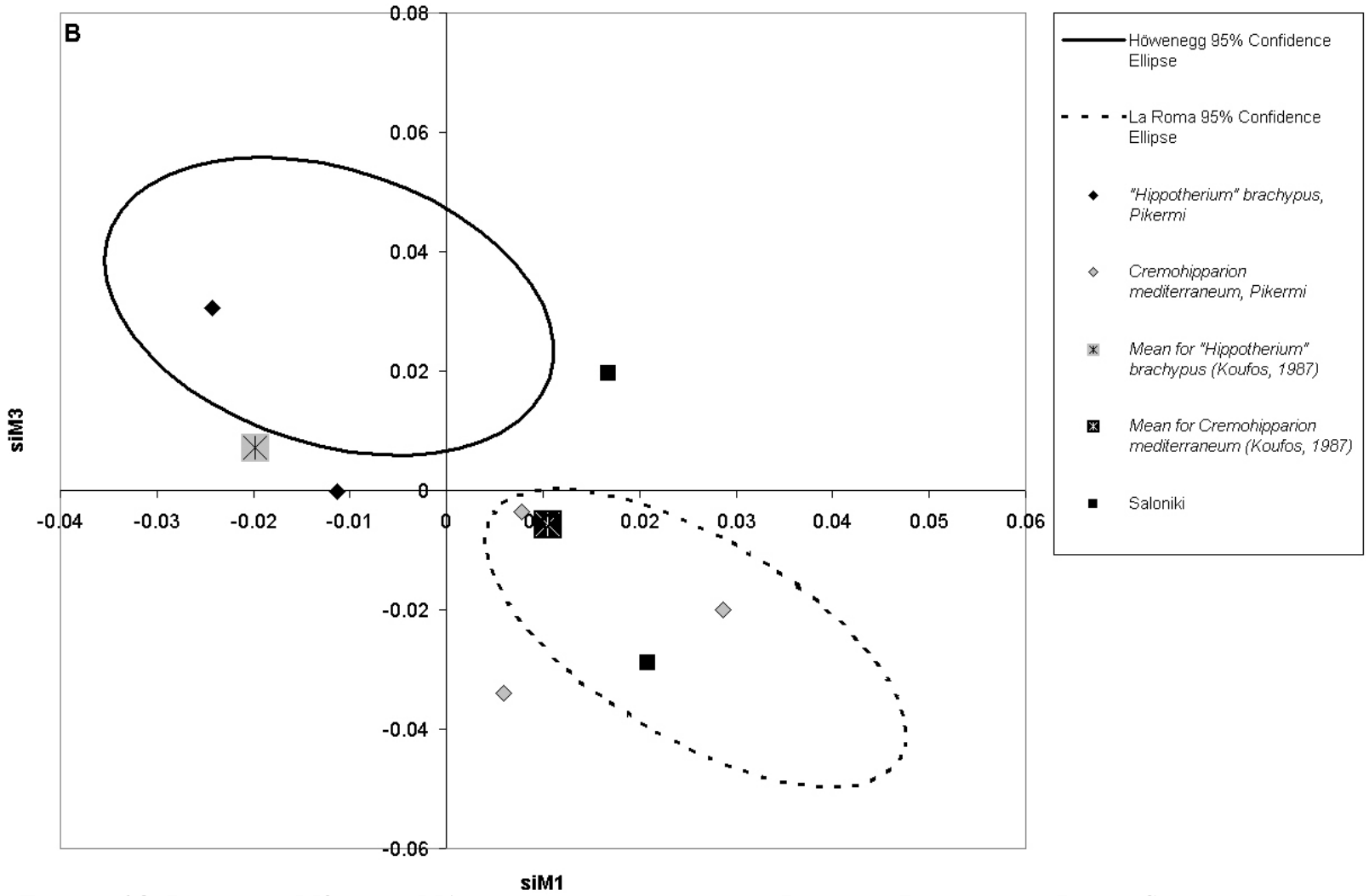


FIGURE 6.8: PLOT OF SIM3 AND SIM1 FOR HIPPARIONINES FROM PIKERMI, RAVIN DE LA PLUIE, SALONIKI, AND MARAMENA. A, MT III's; B, MC III's. Specimens are shown by site and/or possible taxonomic identification with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

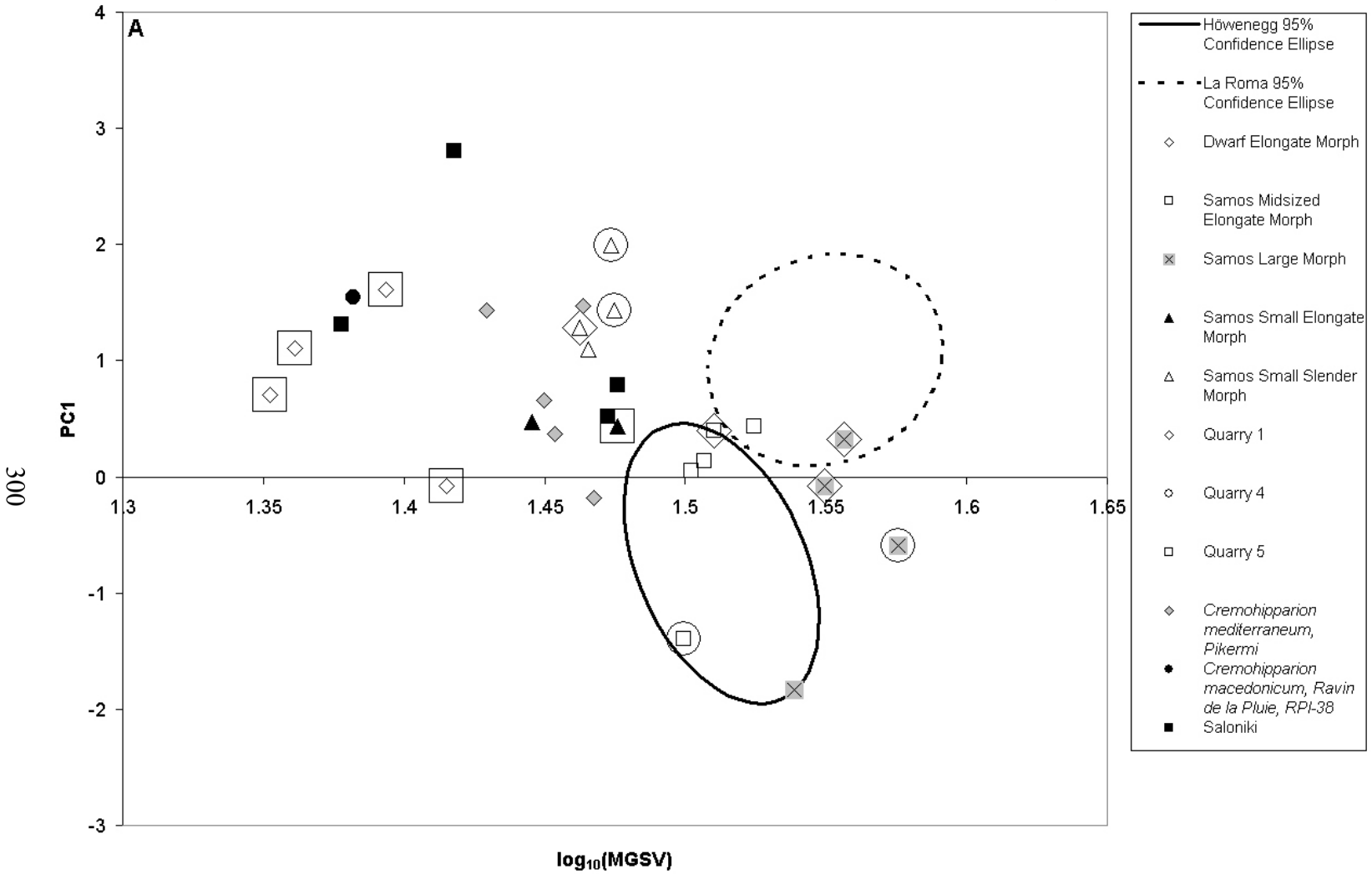
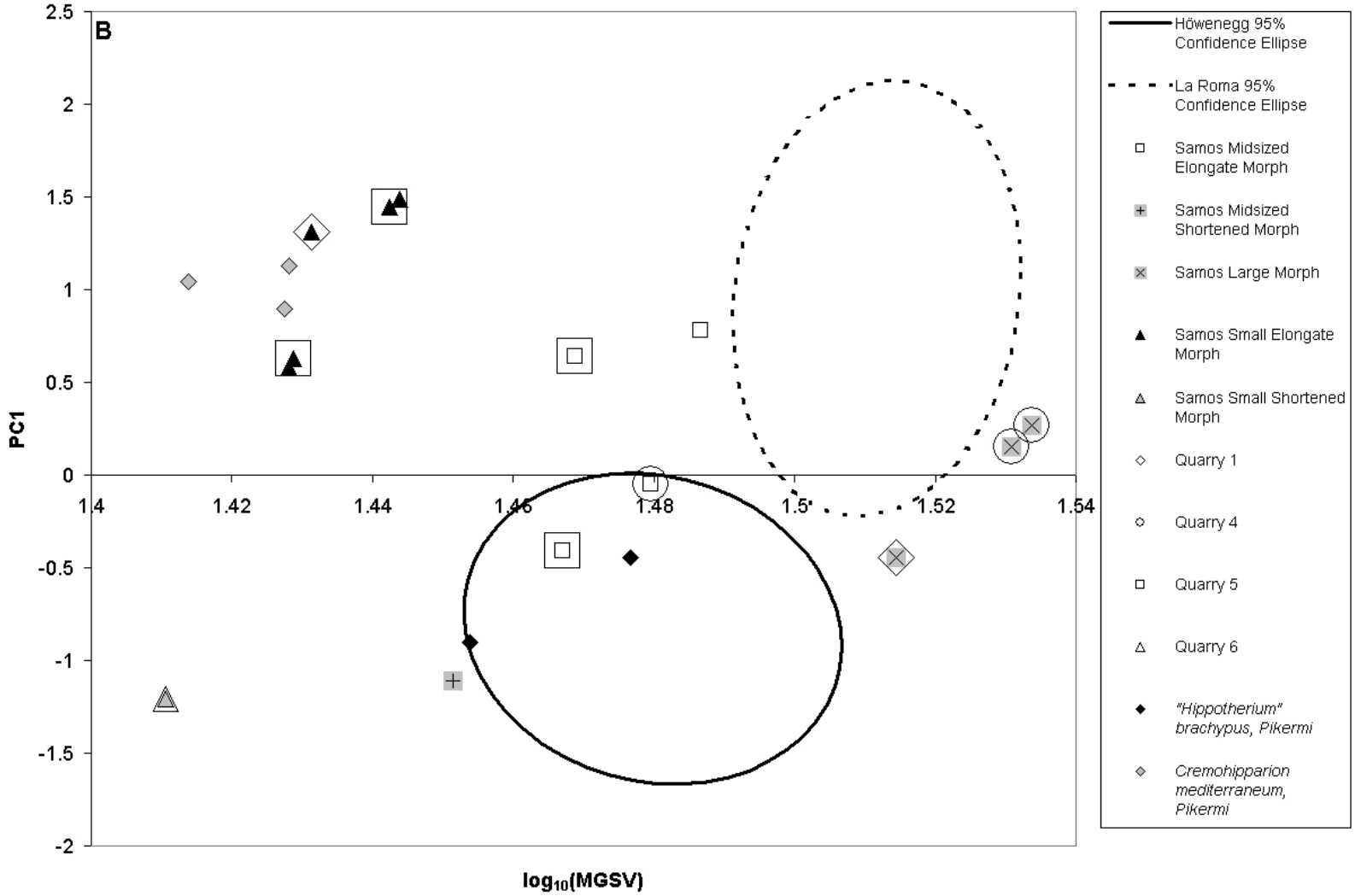


FIGURE 6.9: PLOT OF PC1 AND LOG10(MGSV) FOR HIPPARIONINES FROM SAMOS. A, MT III's; B, MC III's. Specimens are shown by morphological grouping (= Morph) and are plotted with selected comparisons and 95% confidence ellipses for the Höwenegg and La Roma 2. Provenience by Quarry is identified by a separate symbol when



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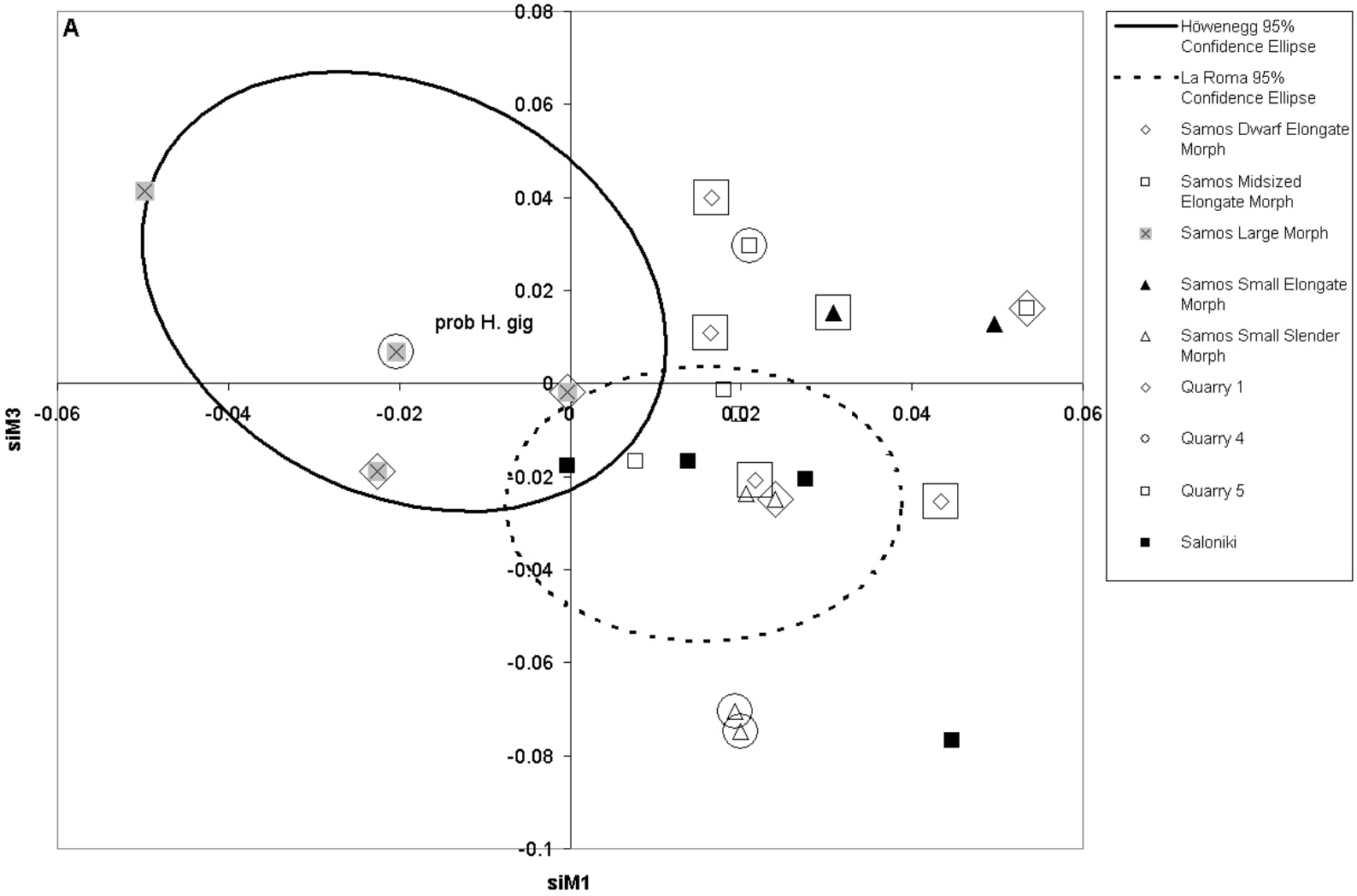


FIGURE 6.10: PLOT OF SIM3 AND SIM1 FOR HIPPARIONINES FROM FROM SAMOS. A, MT III's; B, MC III's. Specimens are shown by morphological grouping (= Morph) and are plotted with selected comparisons and 95% confidence ellipses for the Höwenegg and La Roma 2 standards. Provenience by Quarry is identified by a separate symbol

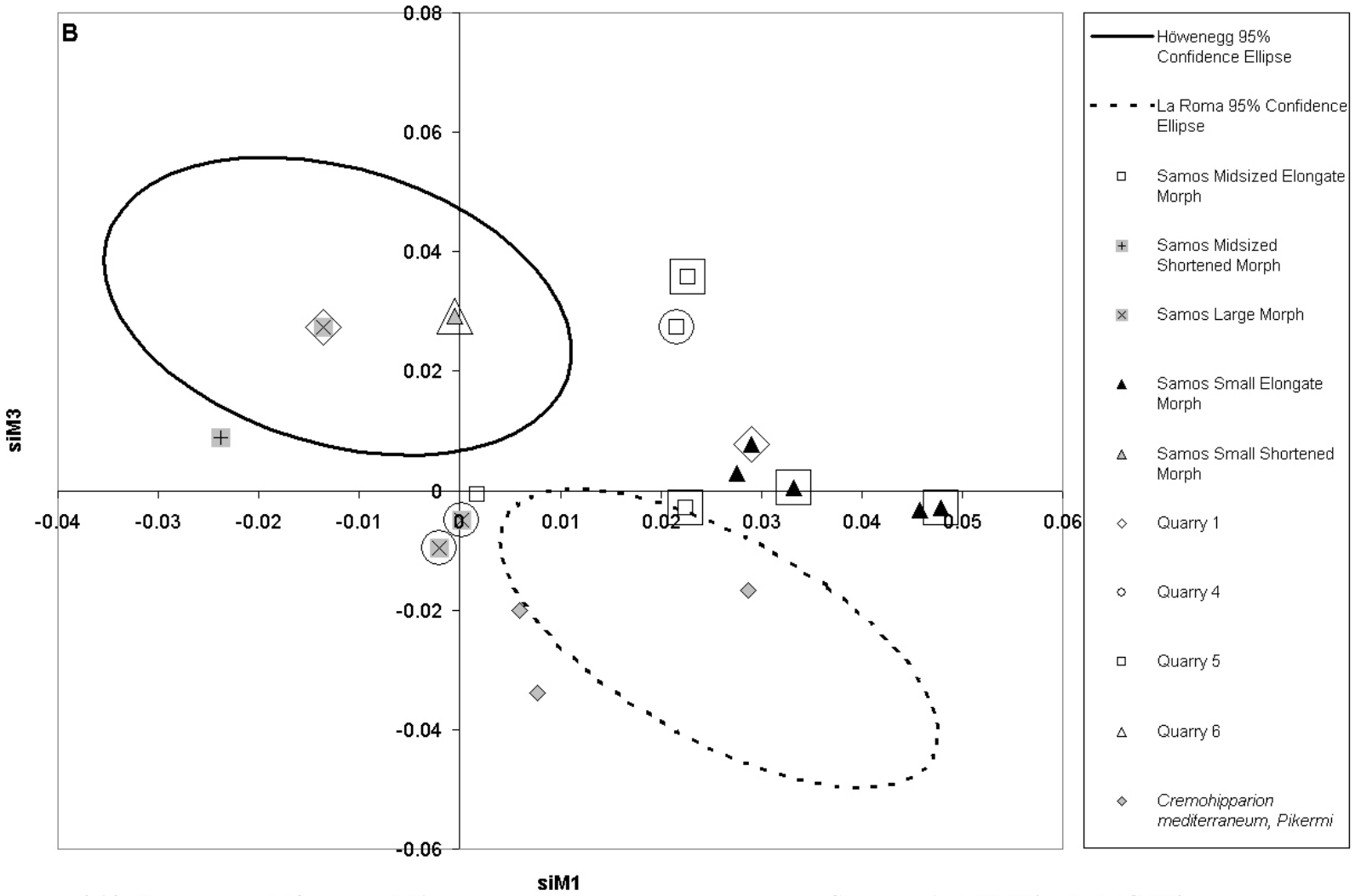


FIGURE 6.10: PLOT OF SIM3 AND SIM1 FOR HIPPARIONINES FROM FROM SAMOS. A, MT III's; B, MC III's. Specimens are shown by morphological grouping (= Morph) and are plotted with selected comparisons and 95% confidence ellipses for the Höwenegg and La Roma 2 standards. Provenience by Quarry is identified by a separate symbol

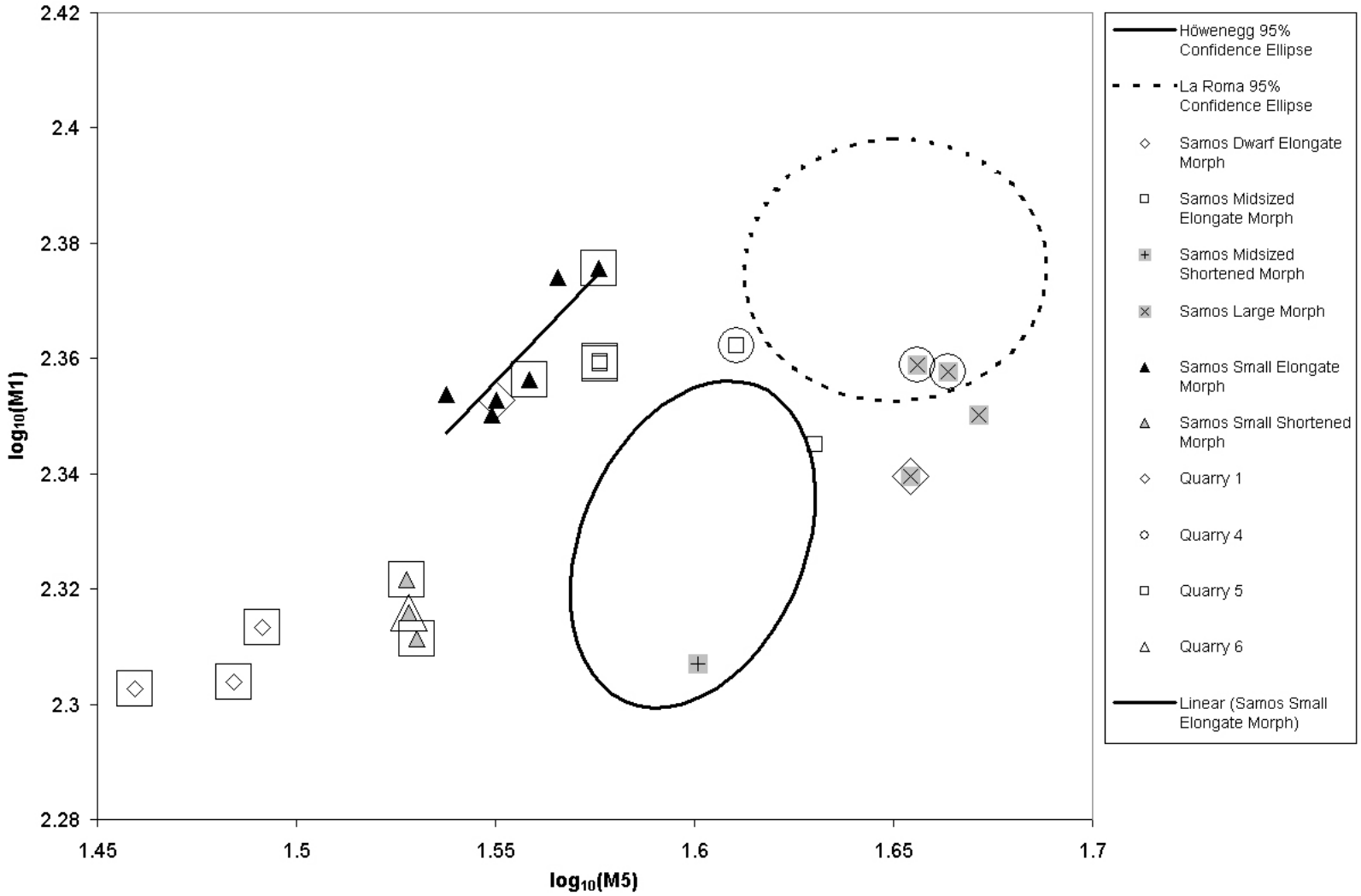


FIGURE 6.11: PLOT OF LOG10(M1) AND LOG10(M5) FOR MC III'S FROM SAMOS. Specimens are shown by morphological grouping (= Morph) and by Quarry when known.

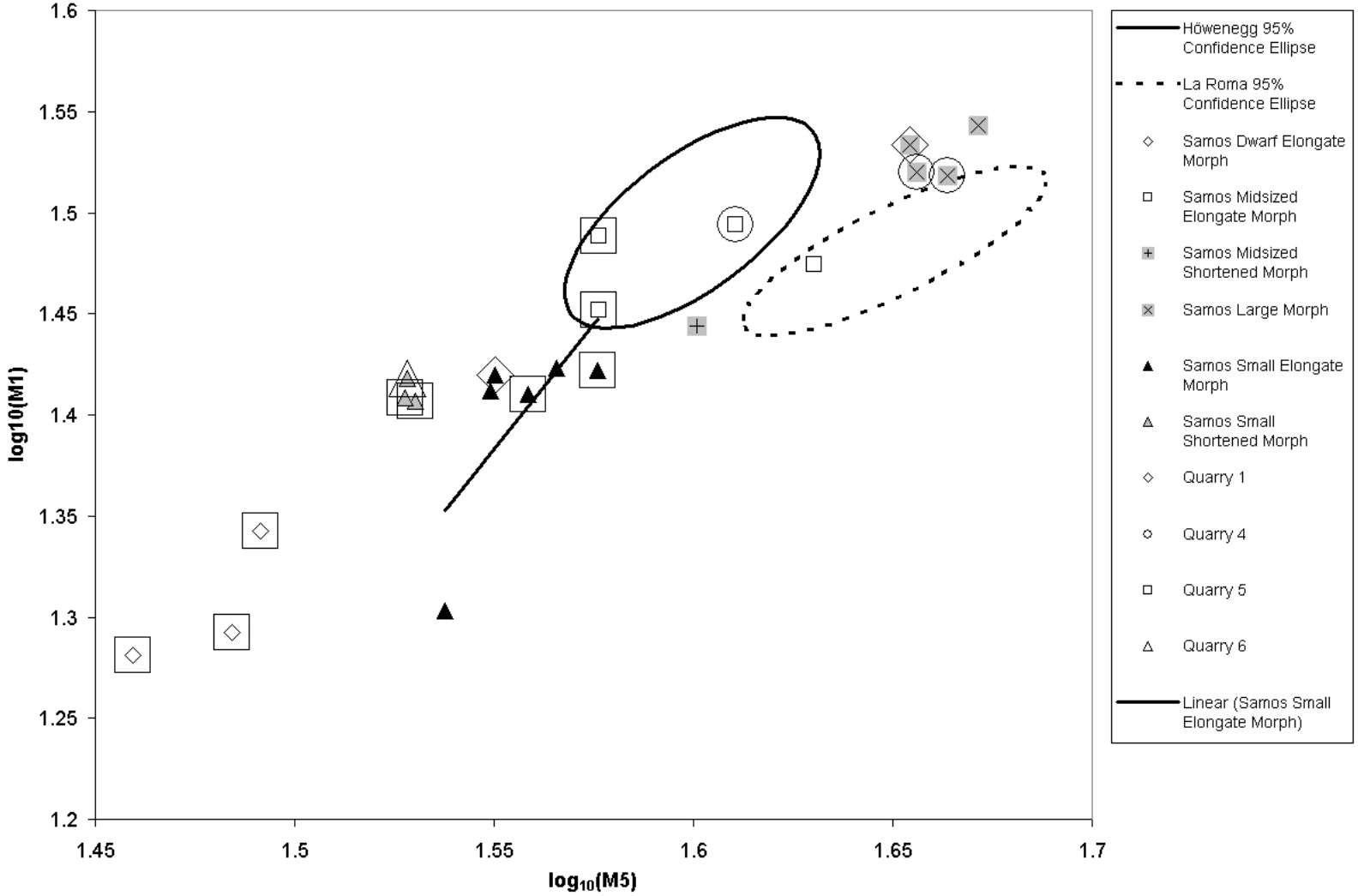


FIGURE 6.12: PLOT OF LOG10(M3) AND LOG10(M5) FOR MC III'S FROM SAMOS. Specimens are shown by morphological grouping (= Morph) and by Quarry when known.

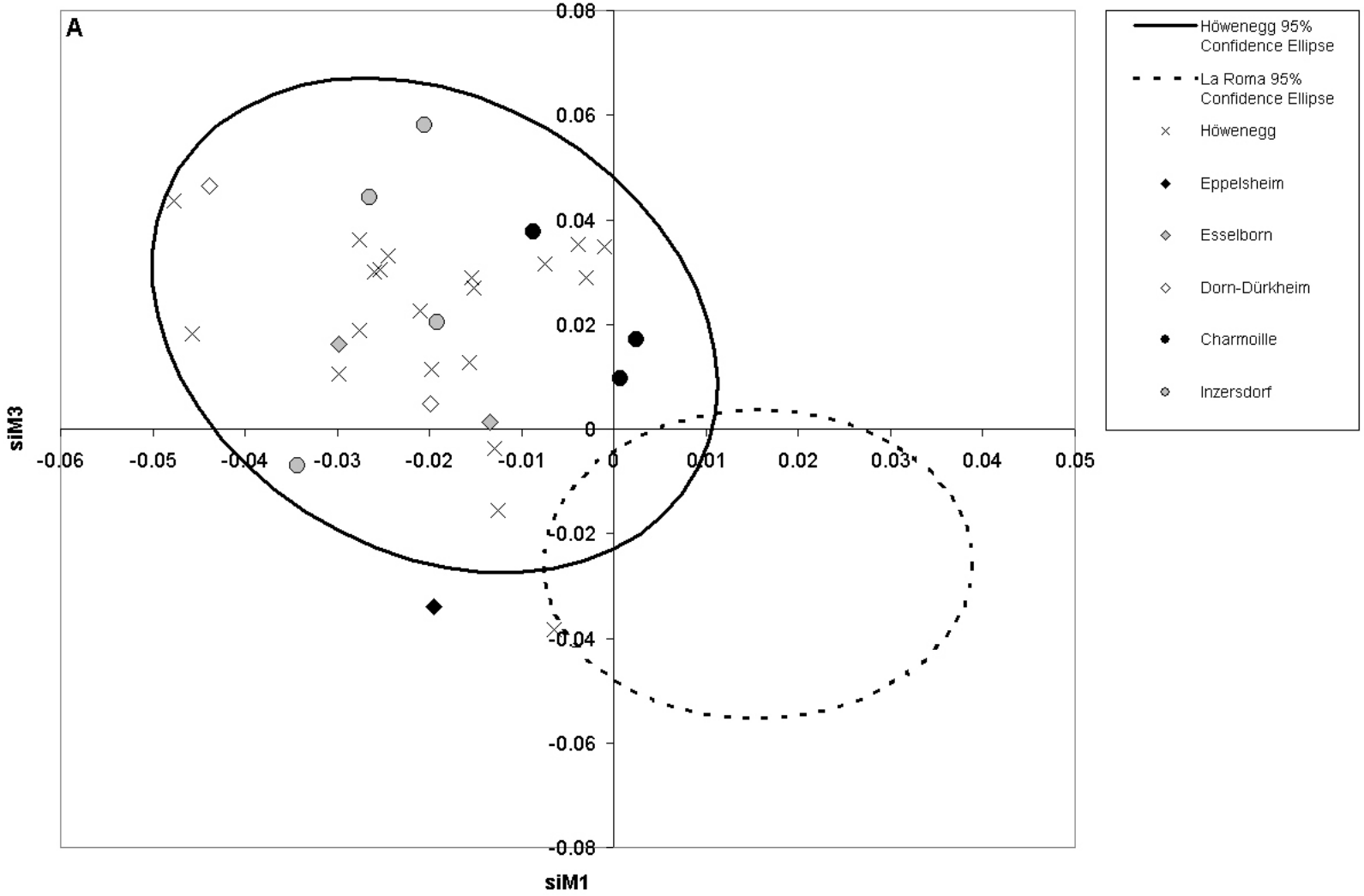


FIGURE 6.13: PLOT OF SIM3 AND SIM1 FOR HIPPARIONINES FROM SELECTED CENTRAL EUROPEAN SITES. A, MT III's; B, MC III's. Specimens are shown by site and/or possible taxonomic identification with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

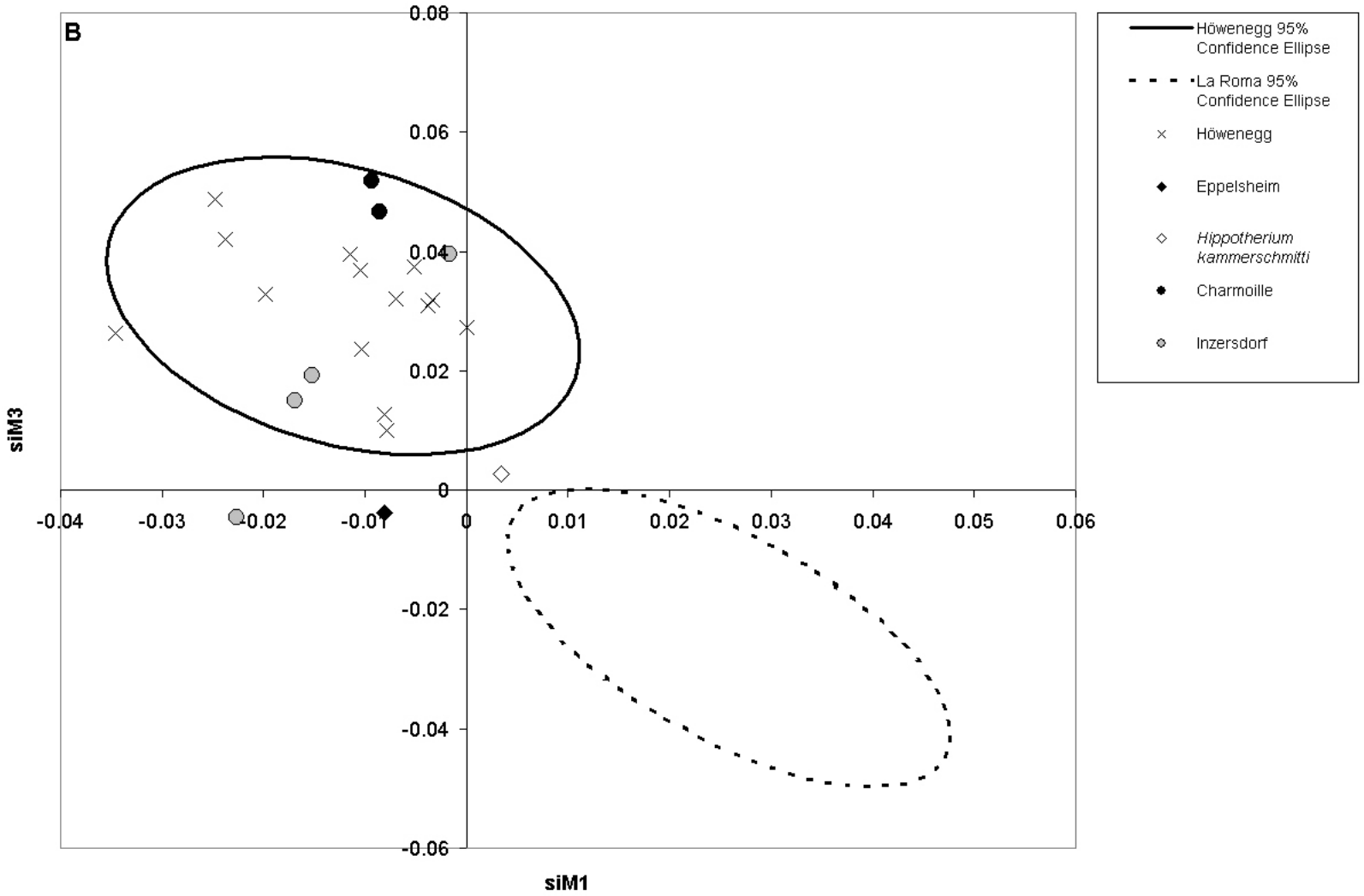


FIGURE 6.13: PLOT OF SIM3 AND SIM1 FOR HIPPARIONINES FROM SELECTED CENTRAL EUROPEAN SITES. A, MT III's; B, MC III's. Specimens are shown by site and/or possible taxonomic identification with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

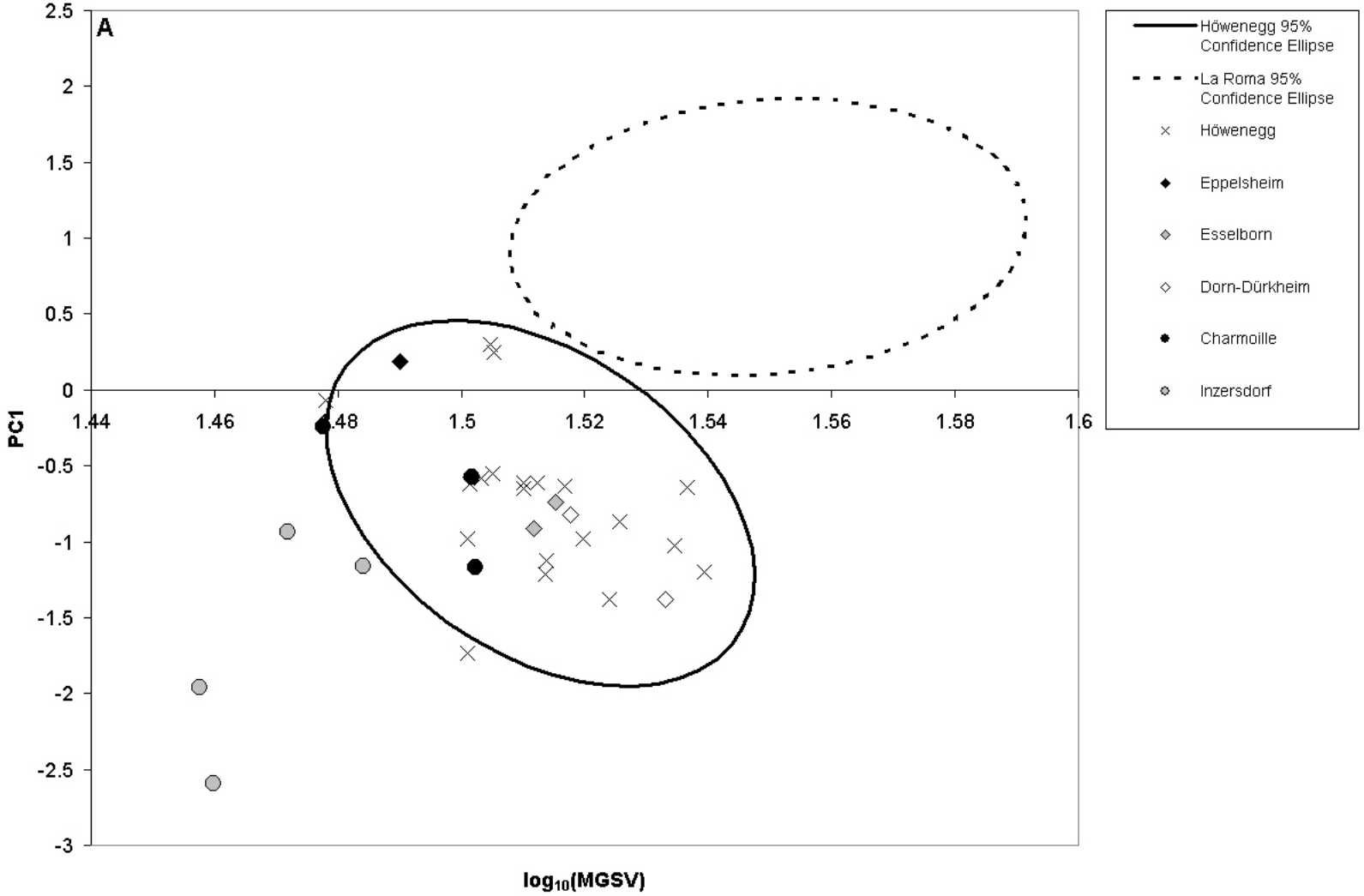


FIGURE 6.14: PLOT OF PC1 AND LOG10(MGSV) FOR HIPPARIONINES FROM SELECTED CENTRAL EUROPEAN SITES. A, MT III's; B, MC III's. Specimens are shown by site and/or possible taxonomic identification with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

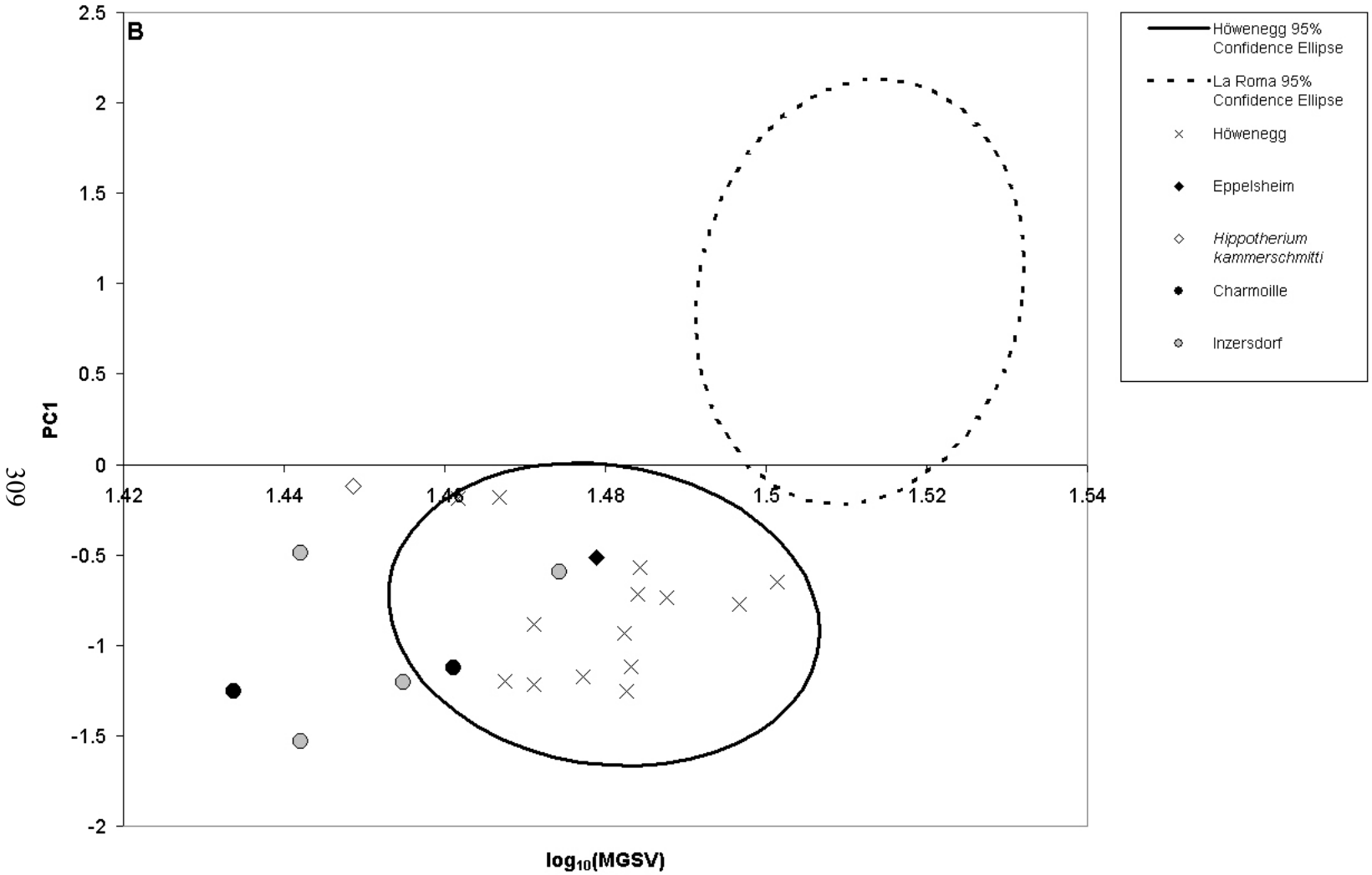


FIGURE 6.14: PLOT OF PC1 AND LOG10(MGSV) FOR HIPPARIONINES FROM SELECTED CENTRAL EUROPEAN SITES. A, MT III's; B, MC III's. Specimens are shown by site and/or possible taxonomic identification with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

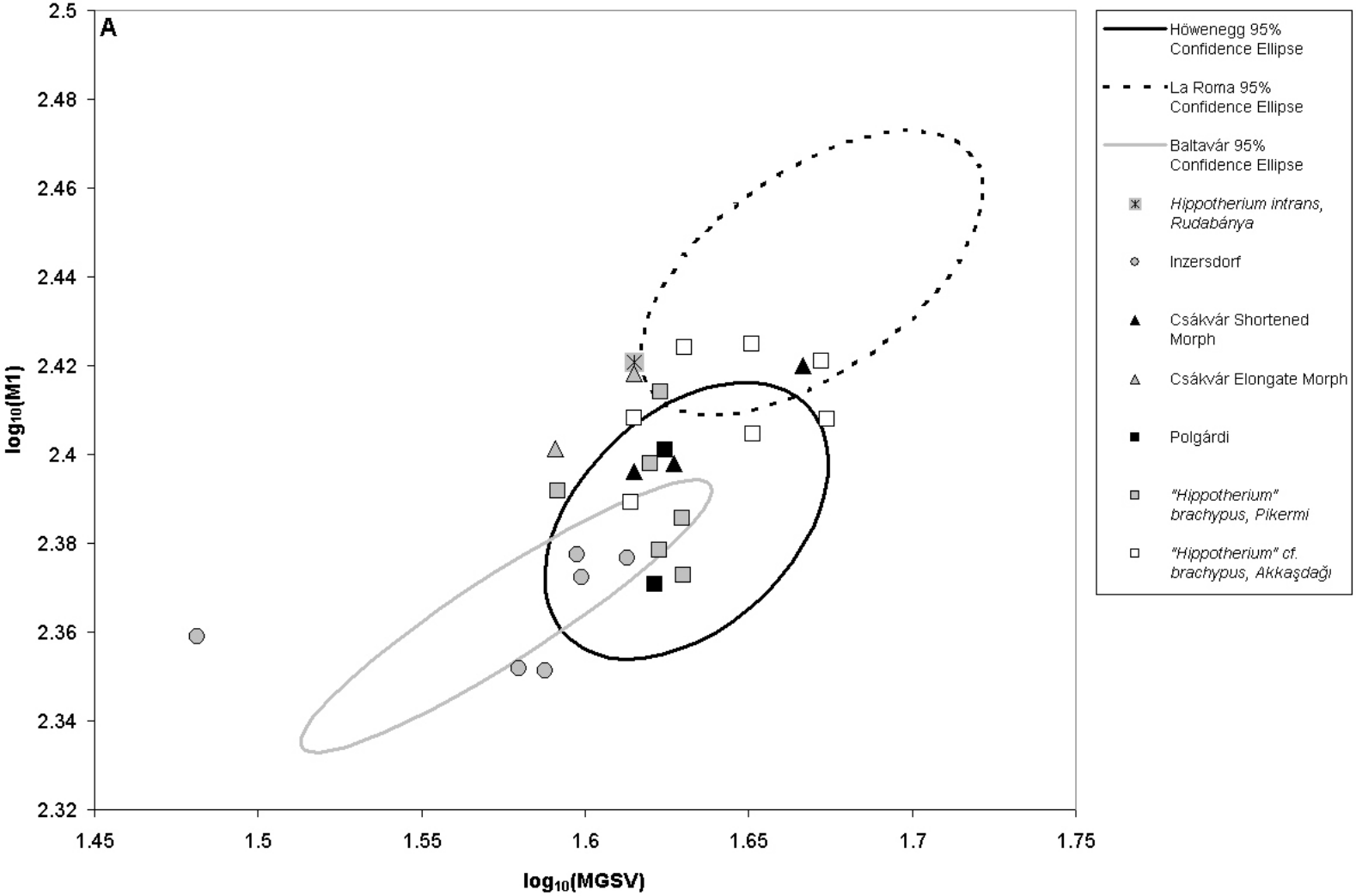


FIGURE 6.15: PLOT OF LOG10(M1) AND LOG10(M5) FOR HIPPARIONINES FROM RUDABÁNYA WITH SELECTED COMPARISONS. A, MT III's; B, MC III's. Specimens are shown by site, morph, and/or possible taxonomic identification with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

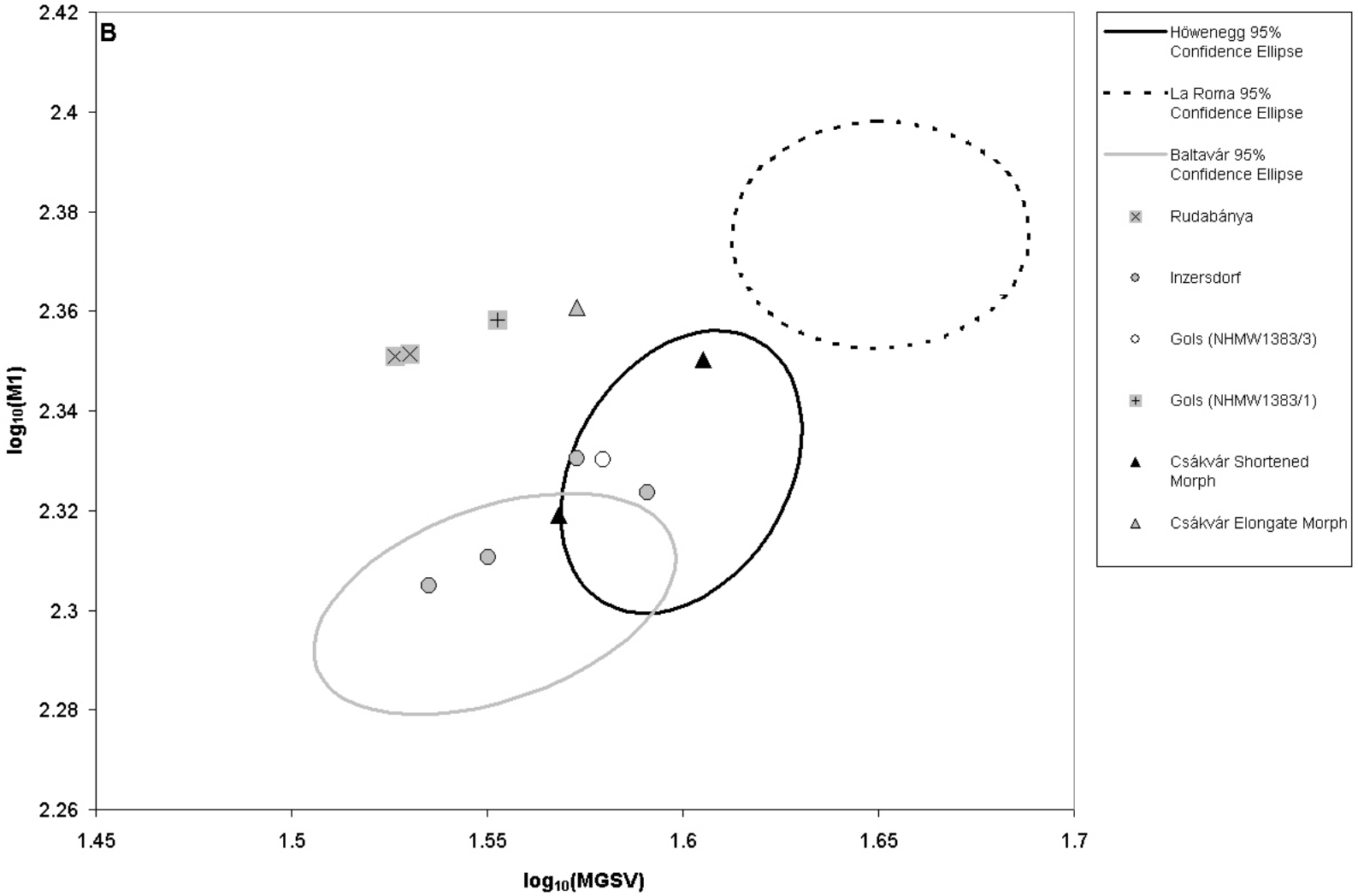


FIGURE 6.15: PLOT OF LOG_{10}(M1) AND LOG_{10}(M5) FOR HIPPARIONINES FROM RUDABÁNYA WITH SELECTED COMPARISONS. A, MT III's; B, MC III's. Specimens are shown by site, morph, and/or possible taxonomic identification with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

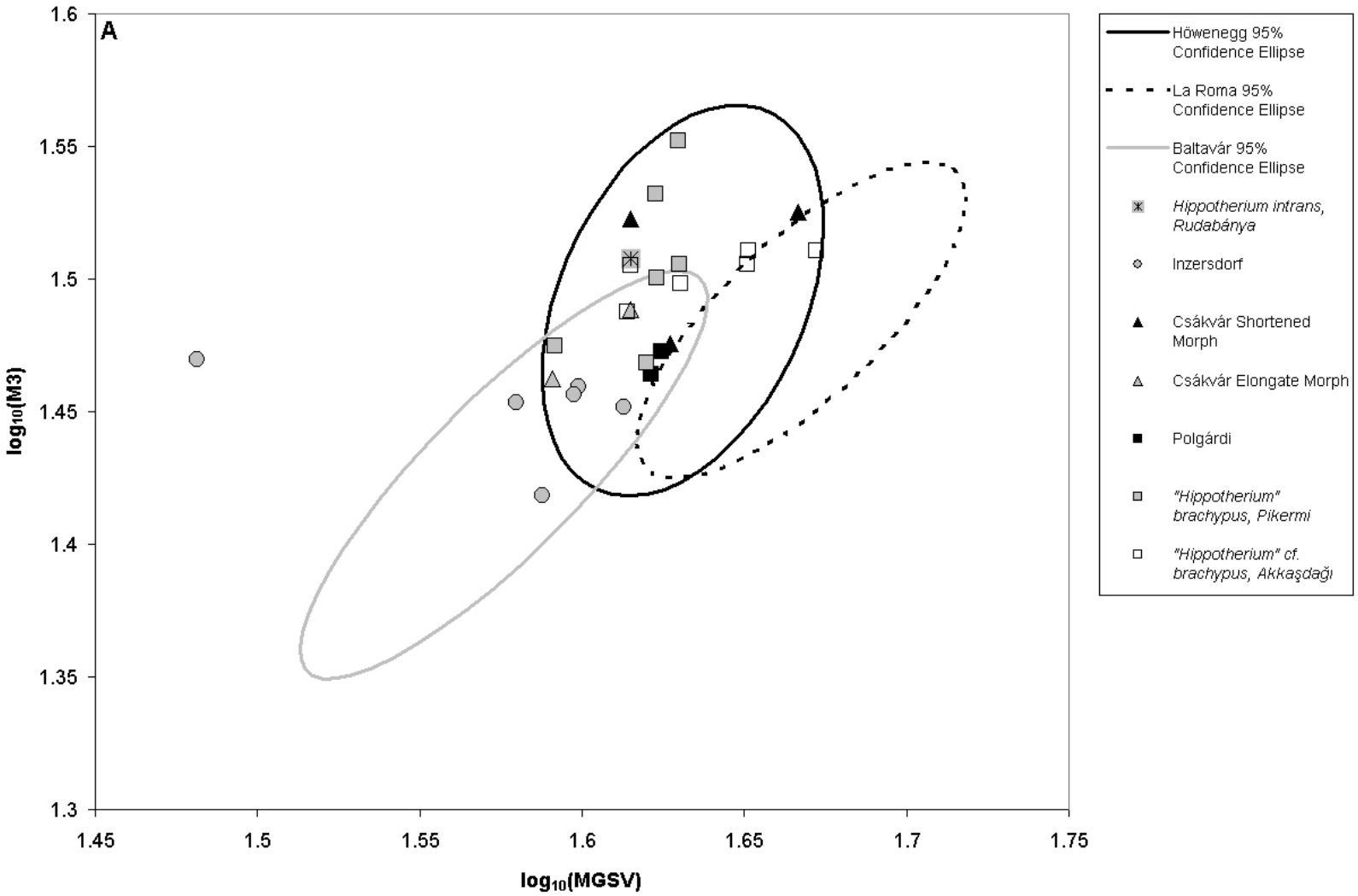


FIGURE 6.16: PLOT OF LOG10(M3) AND LOG10(M5) FOR HIPPARIONINES FROM RUDABÁNYA WITH SELECTED COMPARISONS. A, MT III's; B, MC III's. Specimens are shown by site, morph, and/or possible taxonomic identification with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

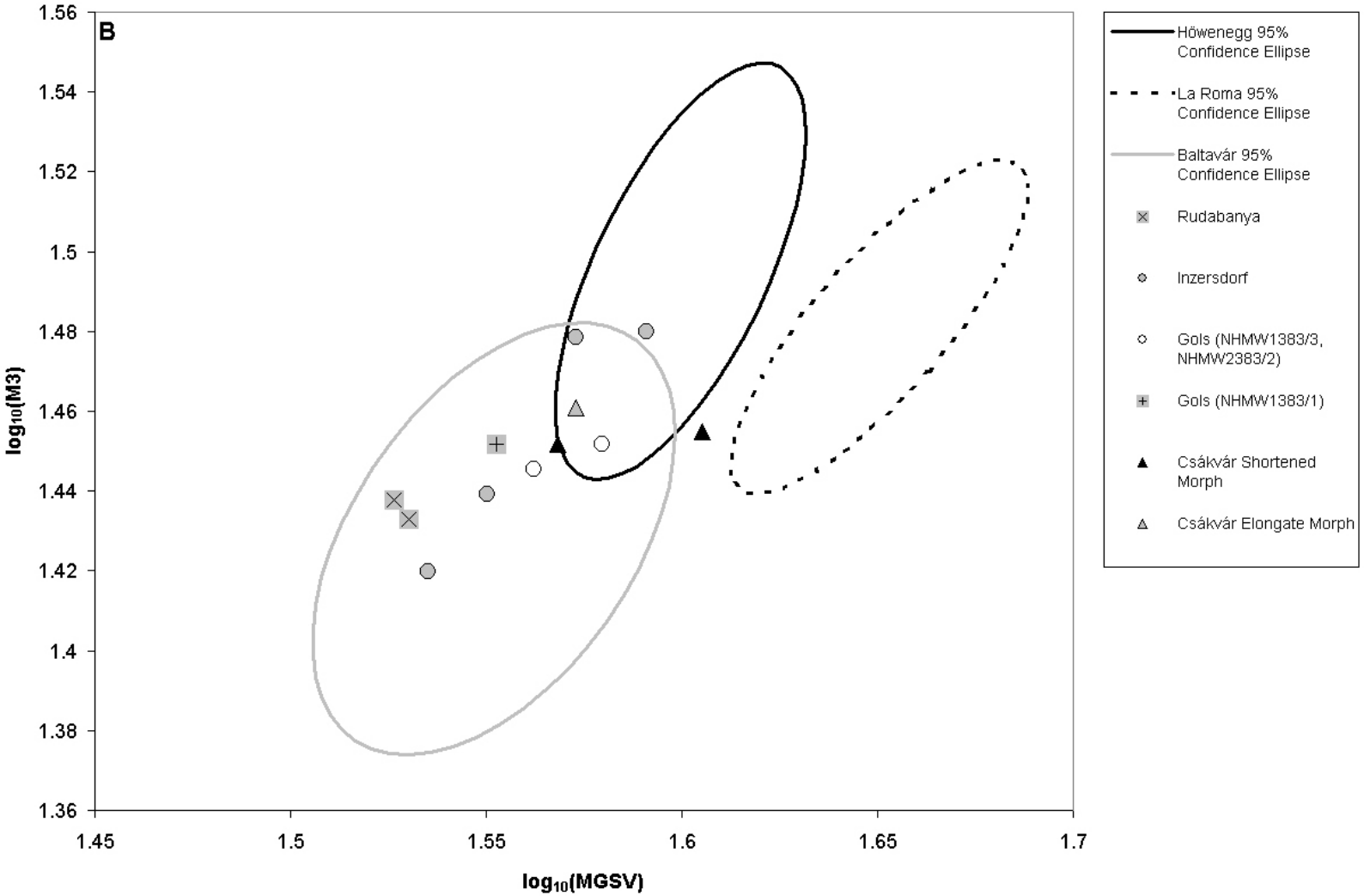


FIGURE 6.16: PLOT OF LOG10(M3) AND LOG10(M5) FOR HIPPARIONINES FROM RUDABÁNYA WITH SELECTED COMPARISONS. A, MT III's; B, MC III's. Specimens are shown by site, morph, and/or possible taxonomic identification with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

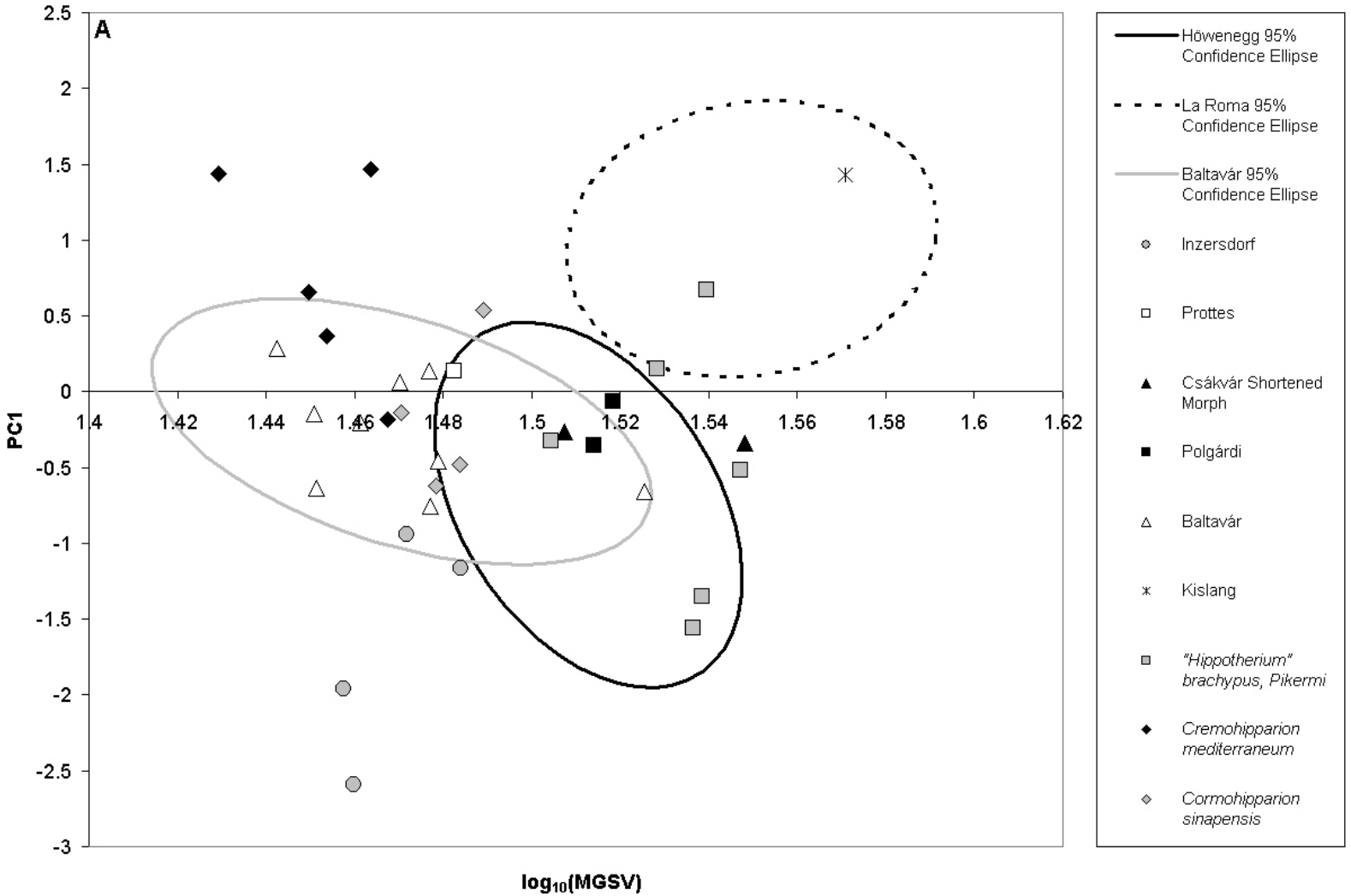


FIGURE 6.17: PLOT OF PC1 AND LOG10(MGSV) FOR HIPPARIONINES FROM THE VIENNA AND PANNONIAN BASINS. A, MT III's; B, MC III's. Specimens are shown by site and/or possible taxonomic identification and are plotted with selected comparisons and 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

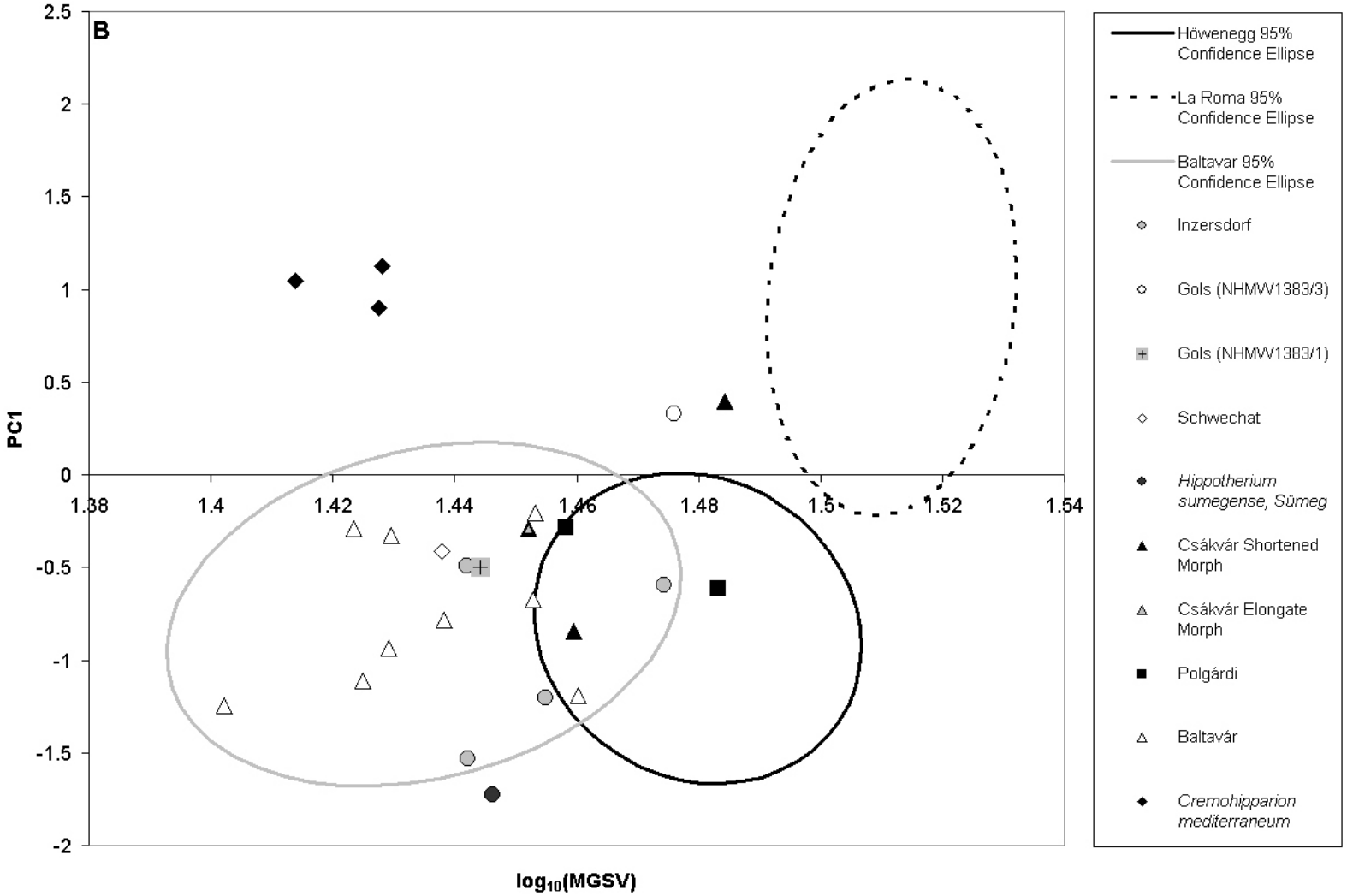


FIGURE 6.17: PLOT OF PC1 AND LOG10(MGSV) FOR HIPPARIONINES FROM THE VIENNA AND PANNONIAN BASINS. A, MT III's; B, MC III's. Specimens are shown by site and/or possible taxonomic identification and are plotted with selected comparisons and 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

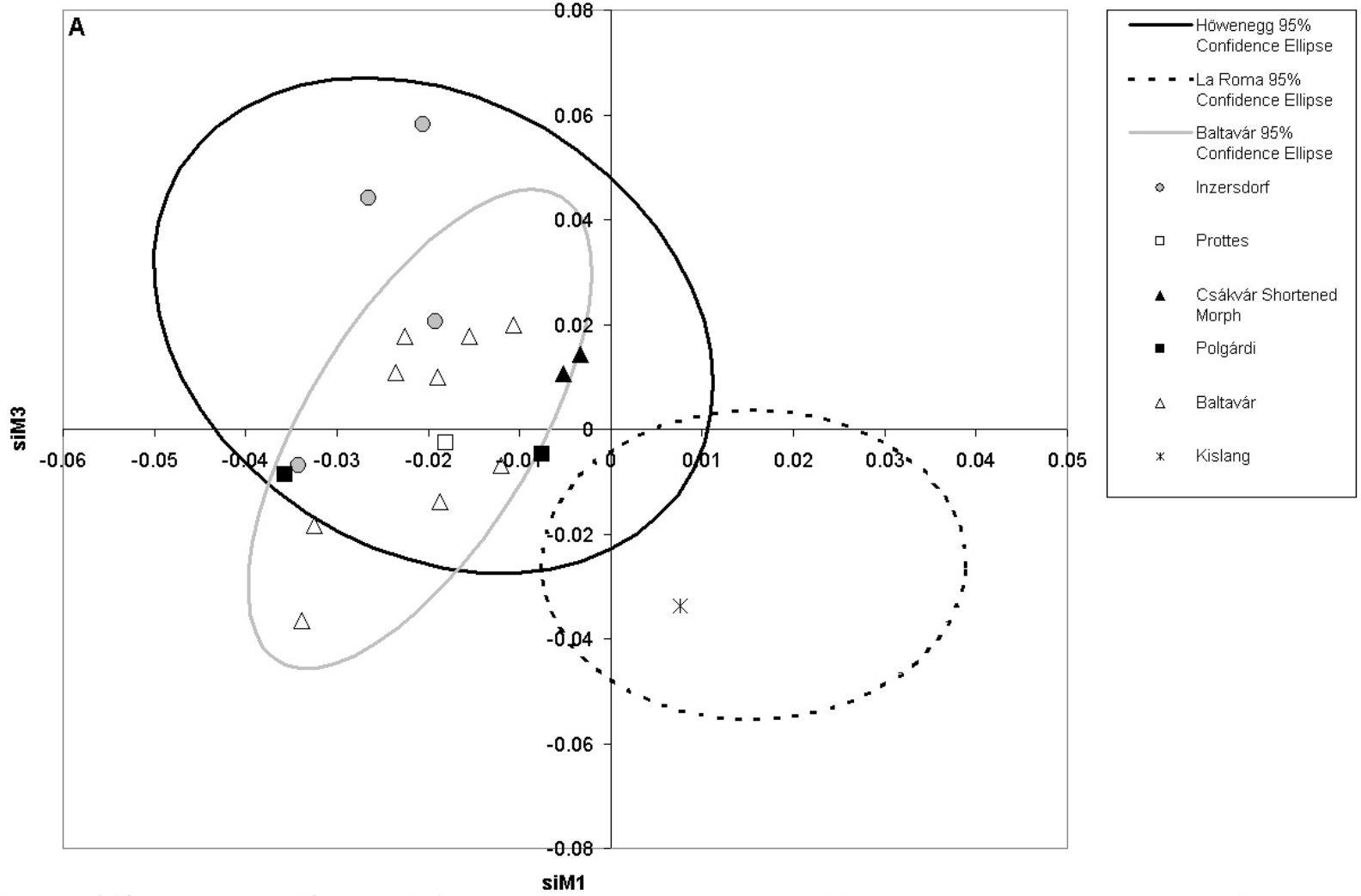


FIGURE 6.18: PLOT OF SIM3 AND SIM1 FOR HIPPARIONINES FROM THE VIENNA AND PANNONIAN BASINS. A, MT III's; B, MC III's. Specimens are shown by site and/or possible taxonomic identification and are plotted with selected comparisons and 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

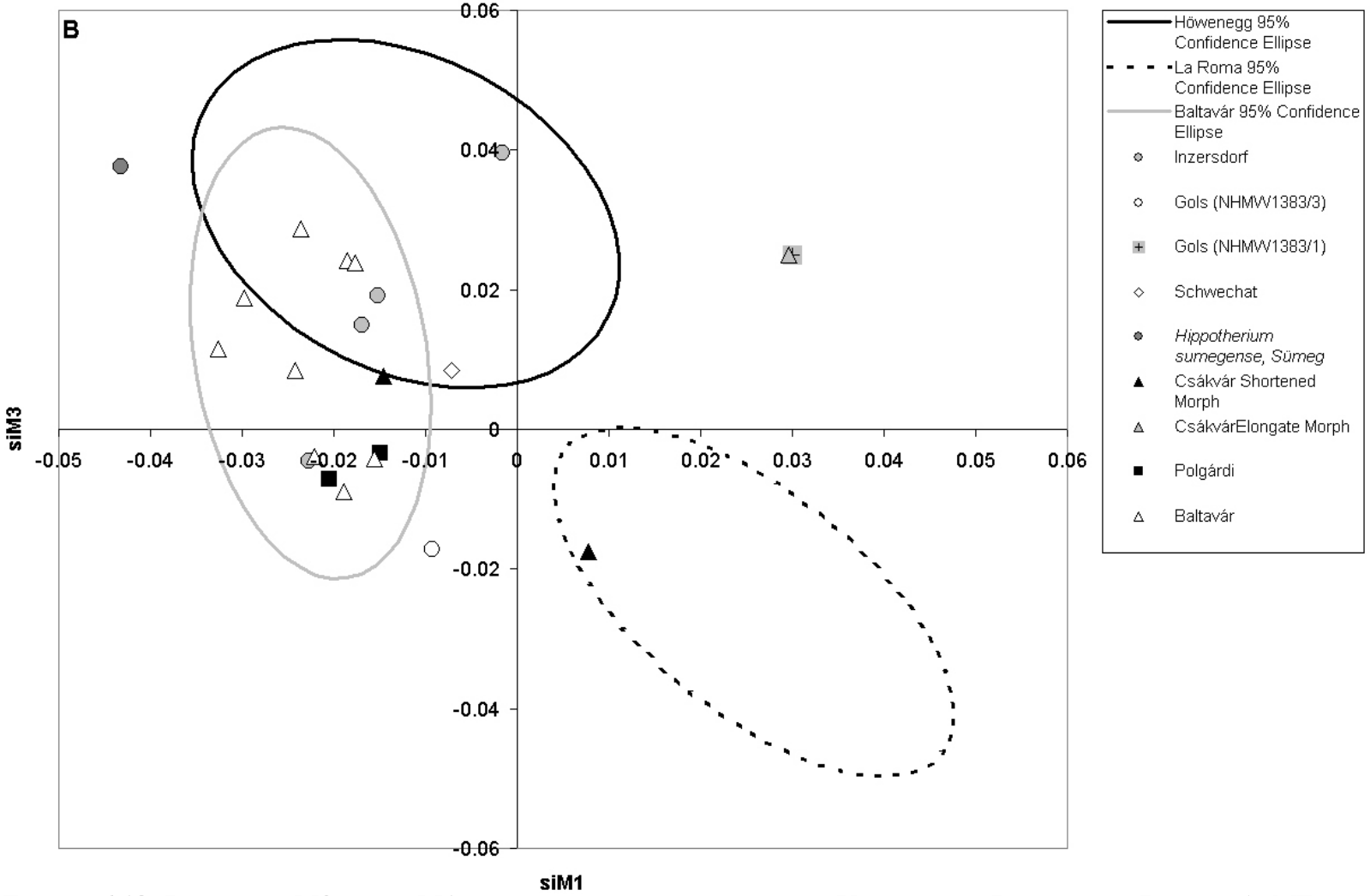


FIGURE 6.18: PLOT OF SIM3 AND SIM1 FOR HIPPARIONINES FROM THE VIENNA AND PANNONIAN BASINS. A, MT III's; B, MC III's. Specimens are shown by site and/or possible taxonomic identification and are plotted with selected comparisons and 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

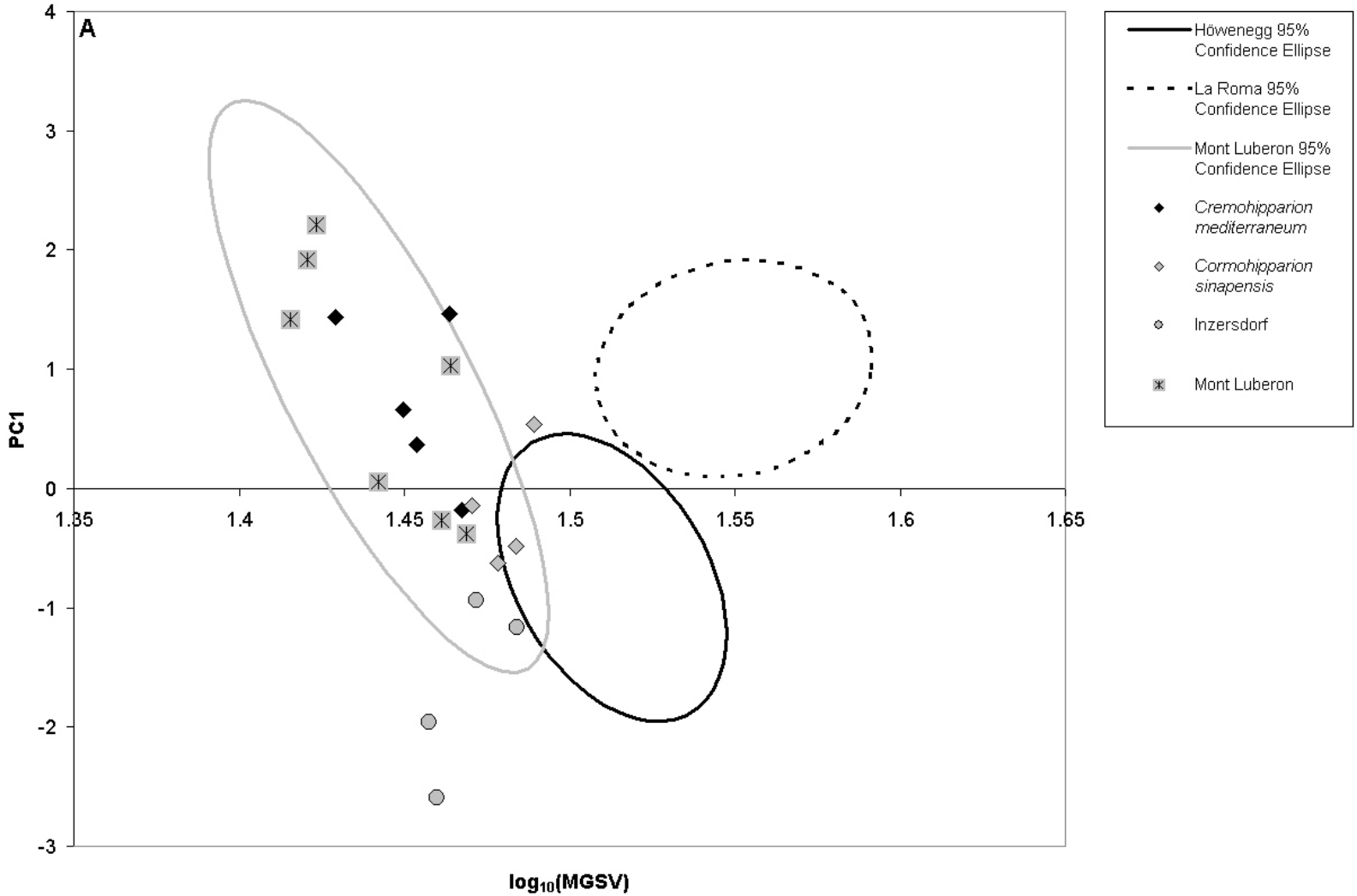


FIGURE 6.19: PLOT OF PC1 AND LOG10(MGSV) FOR HIPPARIONINES FROM MONT LUBERON. A, MT III's; B, MC III's. Specimens are shown by site and/or possible taxonomic identification and are plotted with selected comparisons and 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

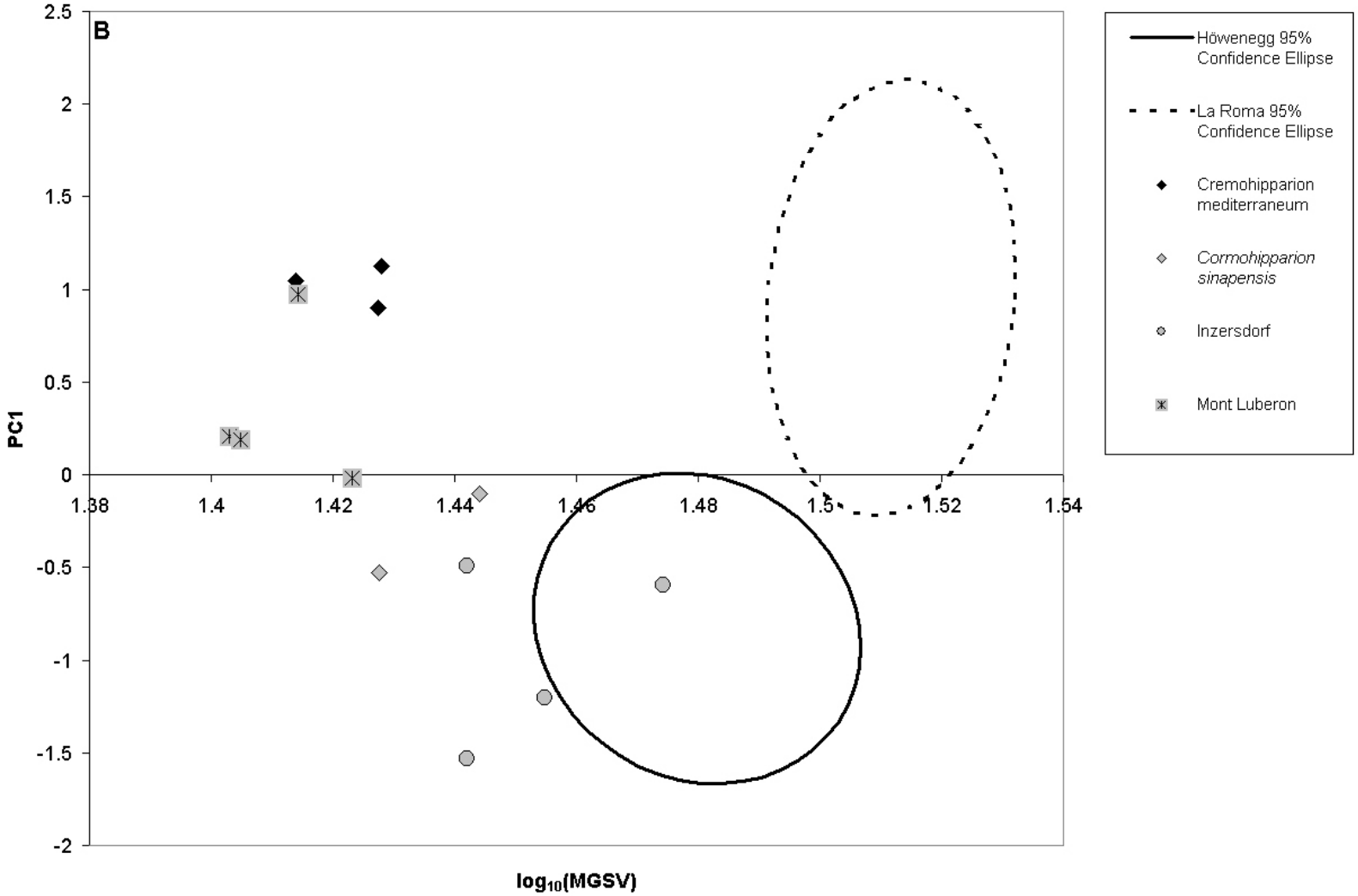


FIGURE 6.19: PLOT OF PC1 AND LOG10(MGSV) FOR HIPPARIONINES FROM MONT LUBERON. A, MT III's; B, MC III's. Specimens are shown by site and/or possible taxonomic identification and are plotted with selected comparisons and 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

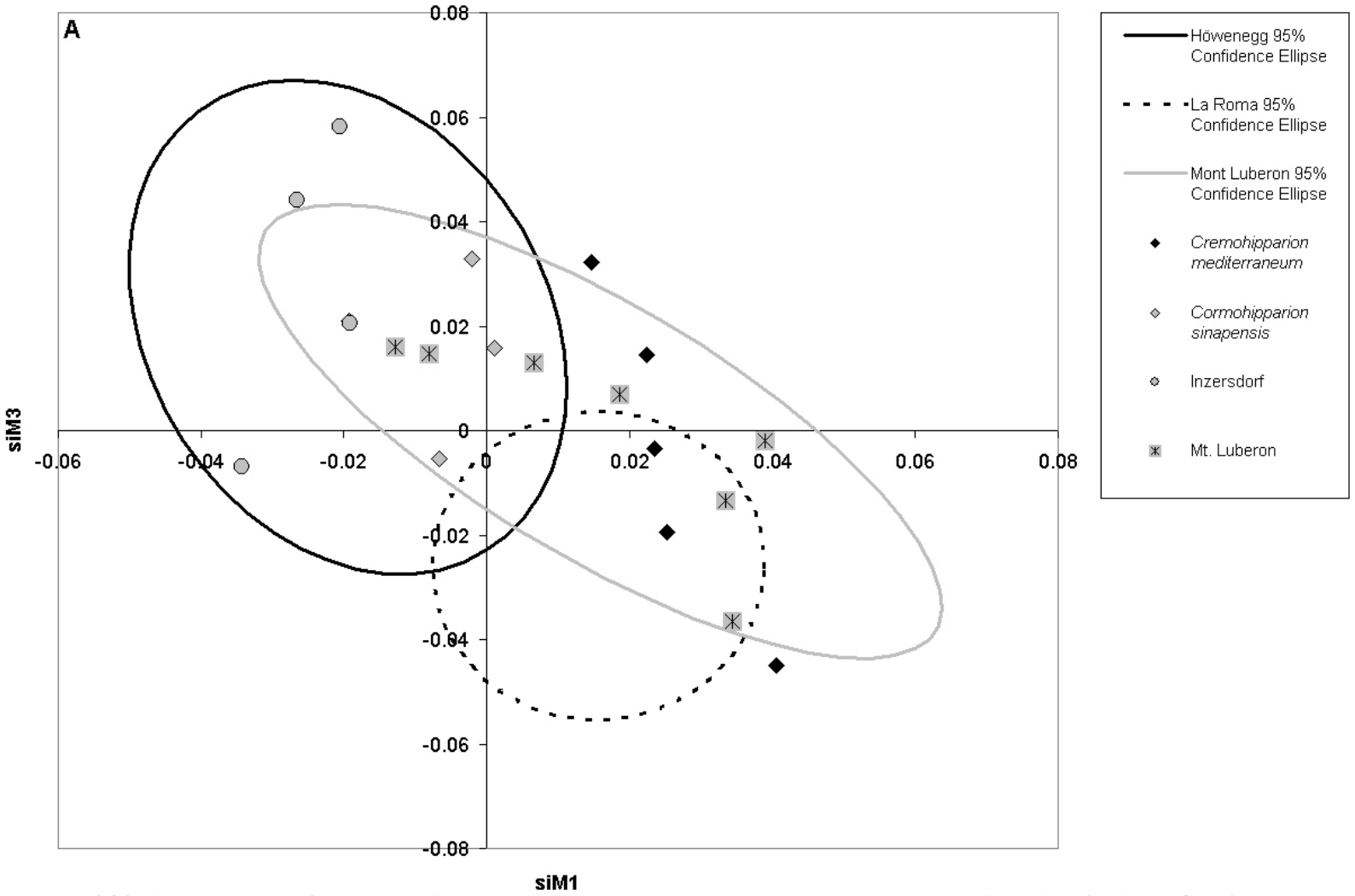


FIGURE 6.20: PLOT OF SIM3 AND SIM1 FOR HIPPARIONINES FROM MONT LUBERON. A, MT III's; B, MC III's. Specimens are shown by site and/or possible taxonomic identification and are plotted with selected comparisons and 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

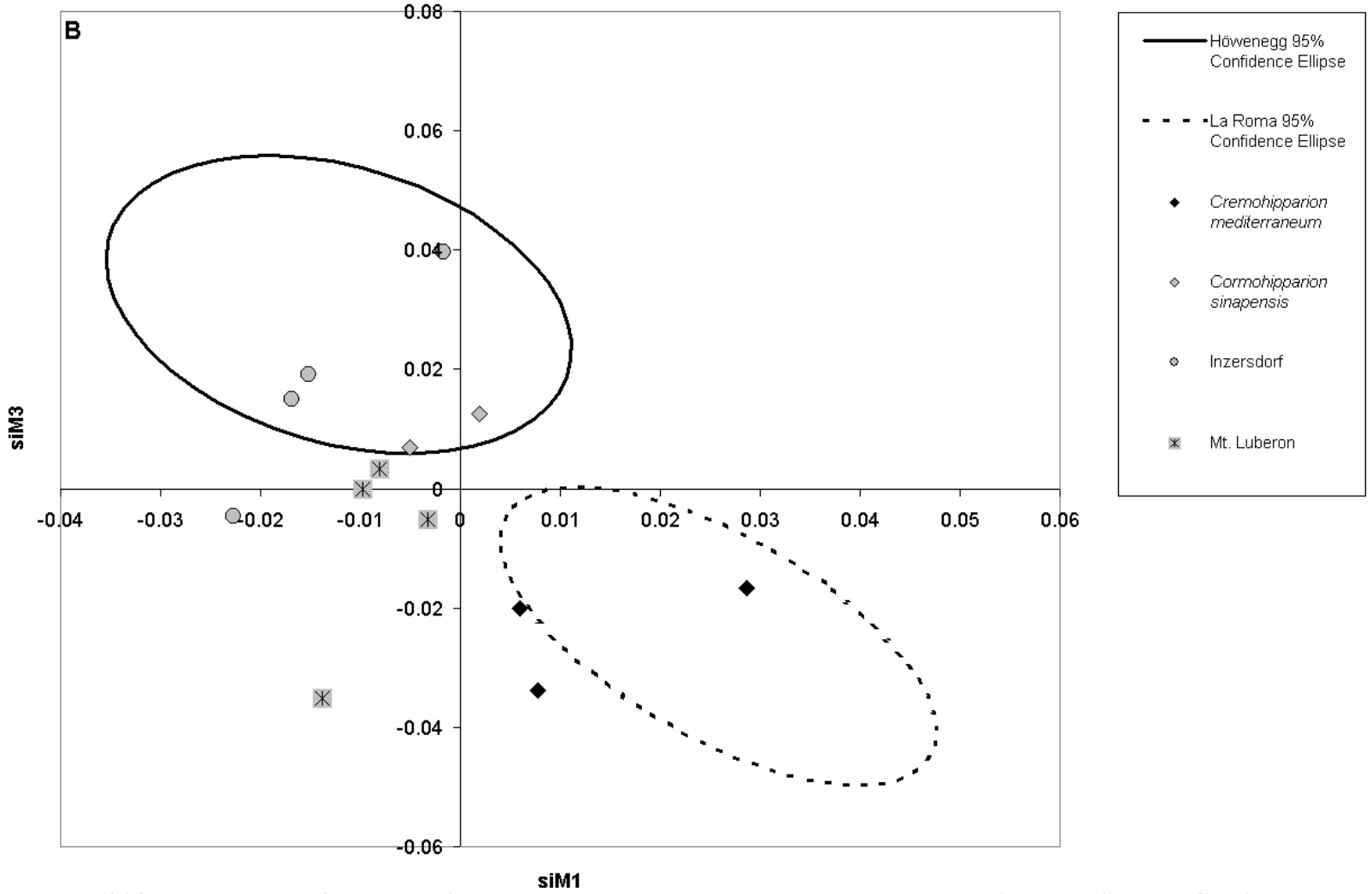


FIGURE 6.20: PLOT OF SIM3 AND SIM1 FOR HIPPARIONINES FROM MONT LUBERON. A, MT III's; B, MC III's. Specimens are shown by site and/or possible taxonomic identification and are plotted with selected comparisons and 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

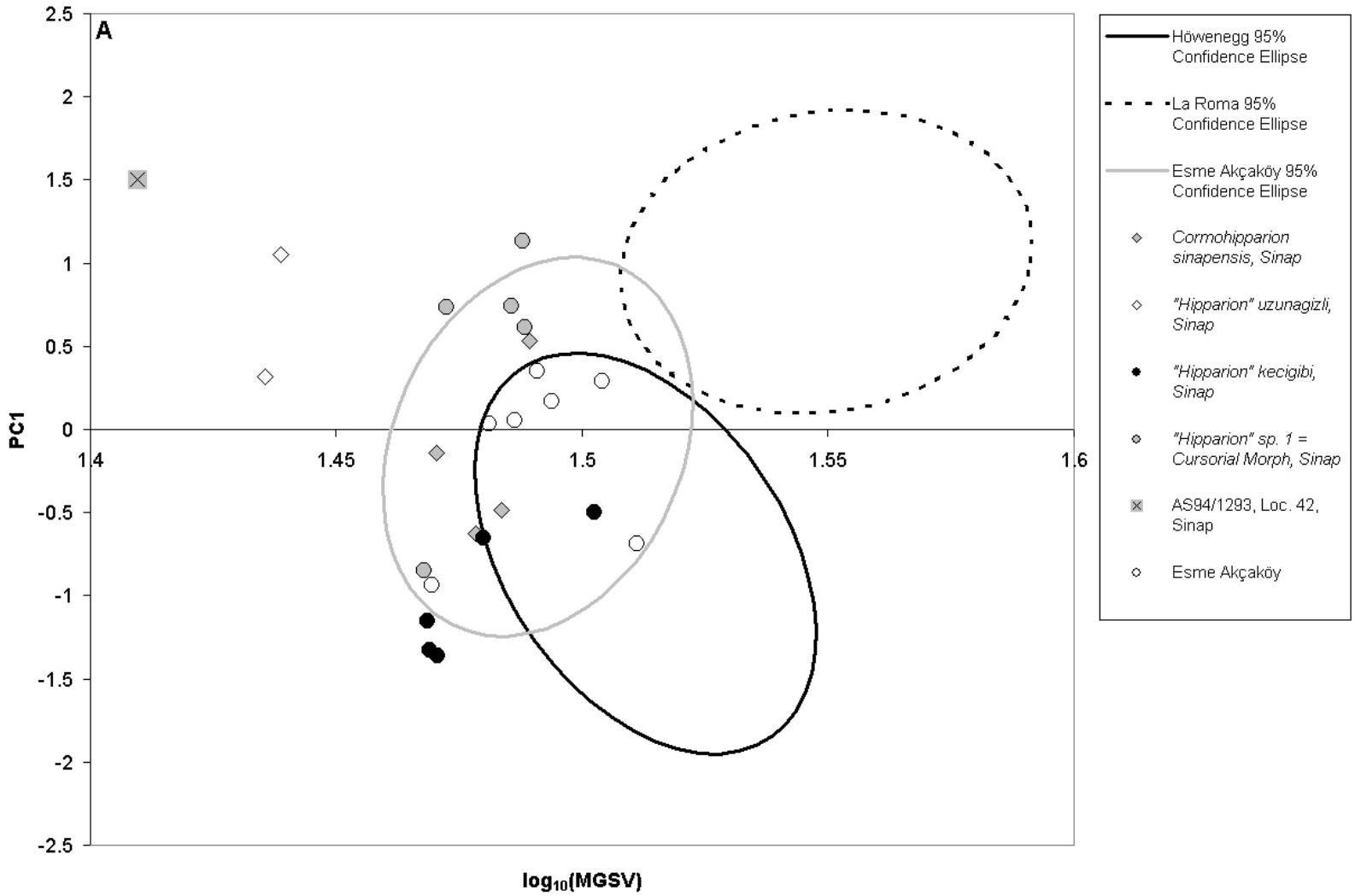


Figure 6.21: Plot of PC1 and log10(MGSV) for hipparionines from Sinap and Esme Akçaköy. A, MT III's; B, MC III's. Specimens are shown by site and/or possible taxonomic identification and are plotted with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

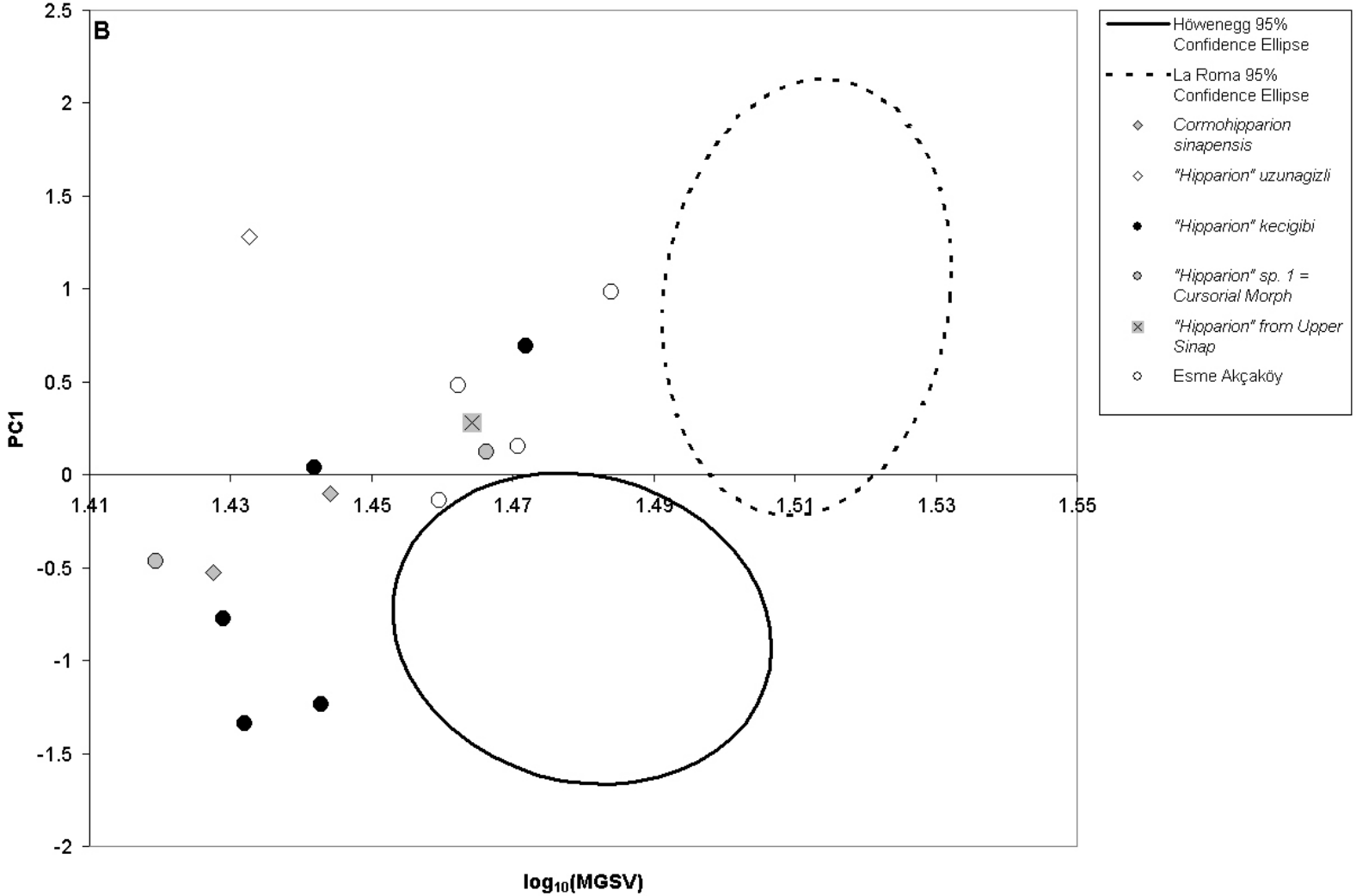


FIGURE 6.21: PLOT OF PC1 AND LOG10(MGSV) FOR HIPPARIONINES FROM SINAP AND ESME AKÇAKÖY. A, MT III's; B, MC III's. Specimens are shown by site and/or possible taxonomic identification and are plotted with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

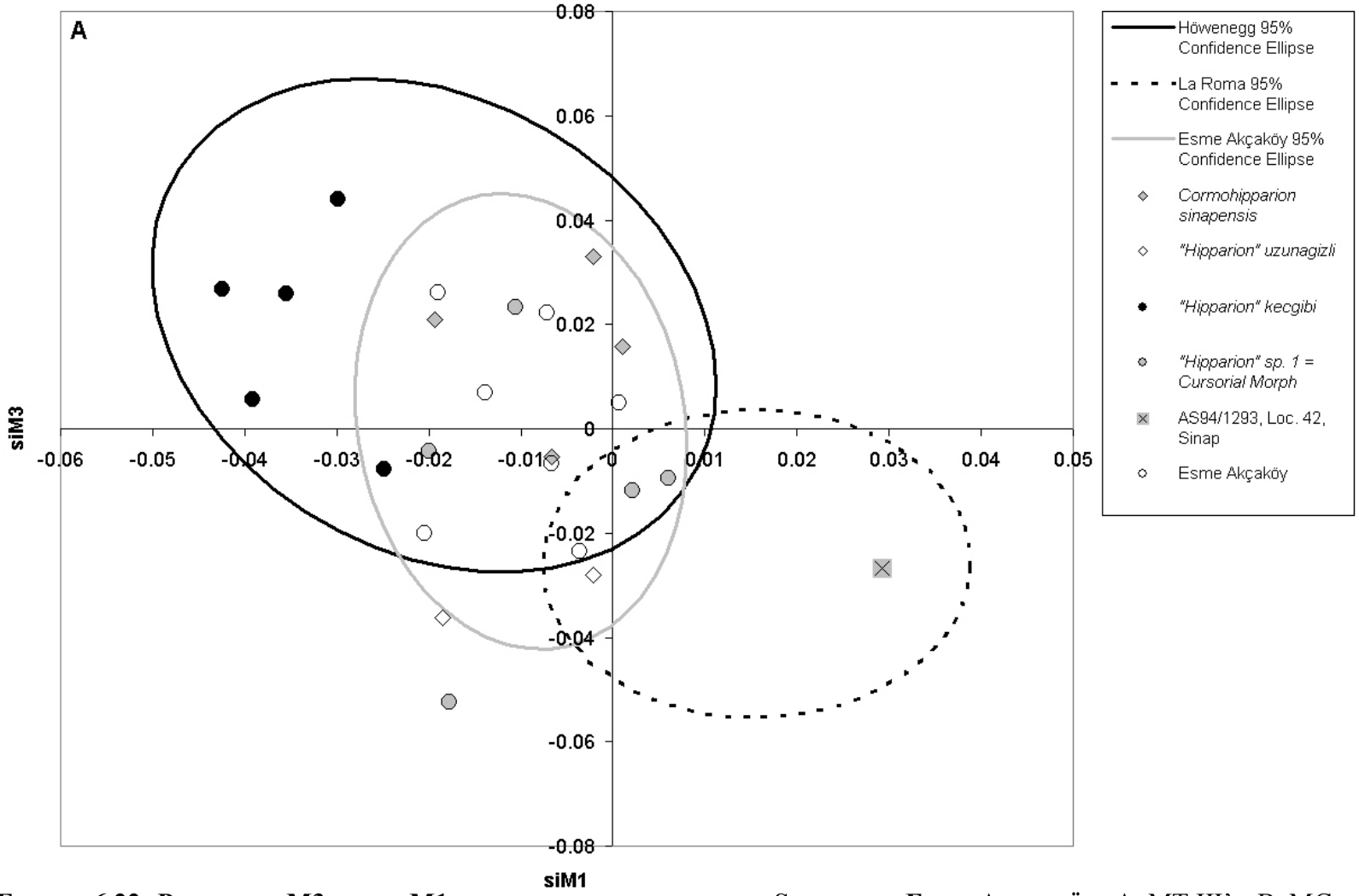


FIGURE 6.22: PLOT OF SIM3 AND SIM1 FOR HIPPARIONINES FROM SINAP AND ESME AKÇAKÖY. A, MT III's; B, MC III's. Specimens are shown by site and/or possible taxonomic identification and are plotted with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

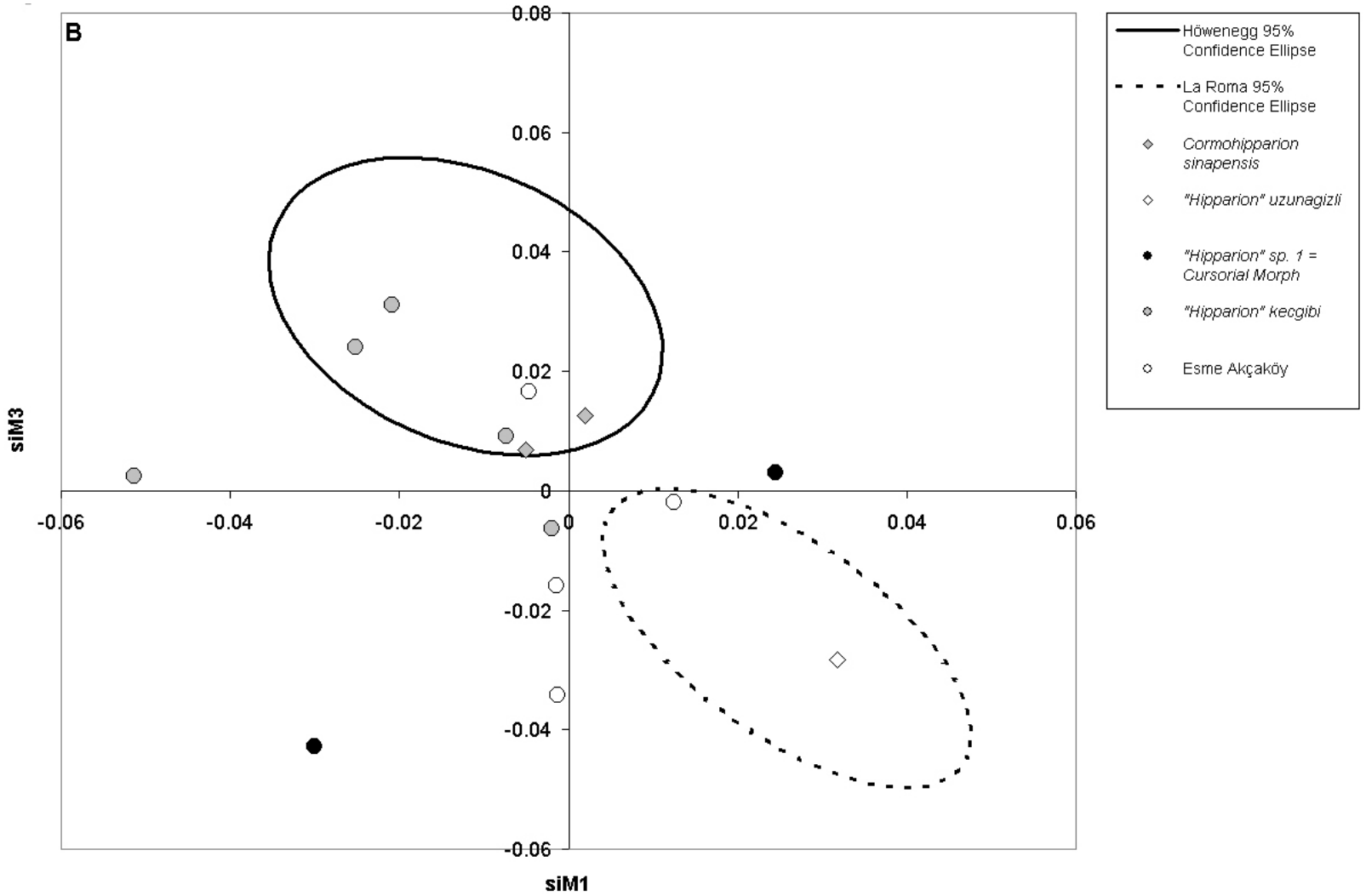


FIGURE 6.22: PLOT OF SIM3 AND SIM1 FOR HIPPARIONINES FROM SINAP AND ESME AKÇAKÖY. A, MT III's; B, MC III's. Specimens are shown by site and/or possible taxonomic identification and are plotted with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

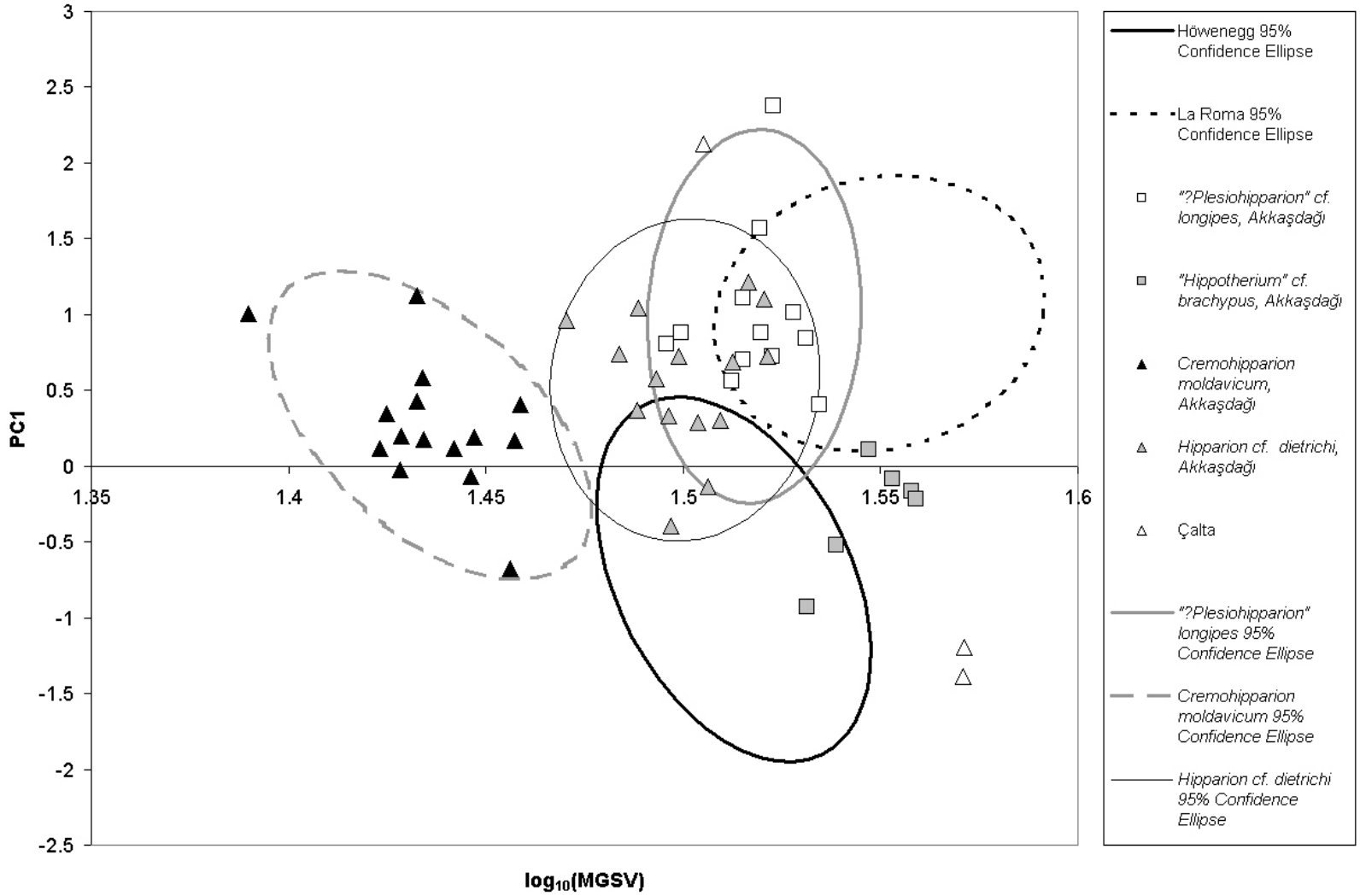


FIGURE 6.23: PLOT OF PC1 AND LOG10(MGSV) FOR HIPPARIONINES FROM AKKAŞDAĞI AND ÇALTA. A, MT III's; B, MC III's. Specimens are shown by site and/or possible taxonomic identification and are plotted with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

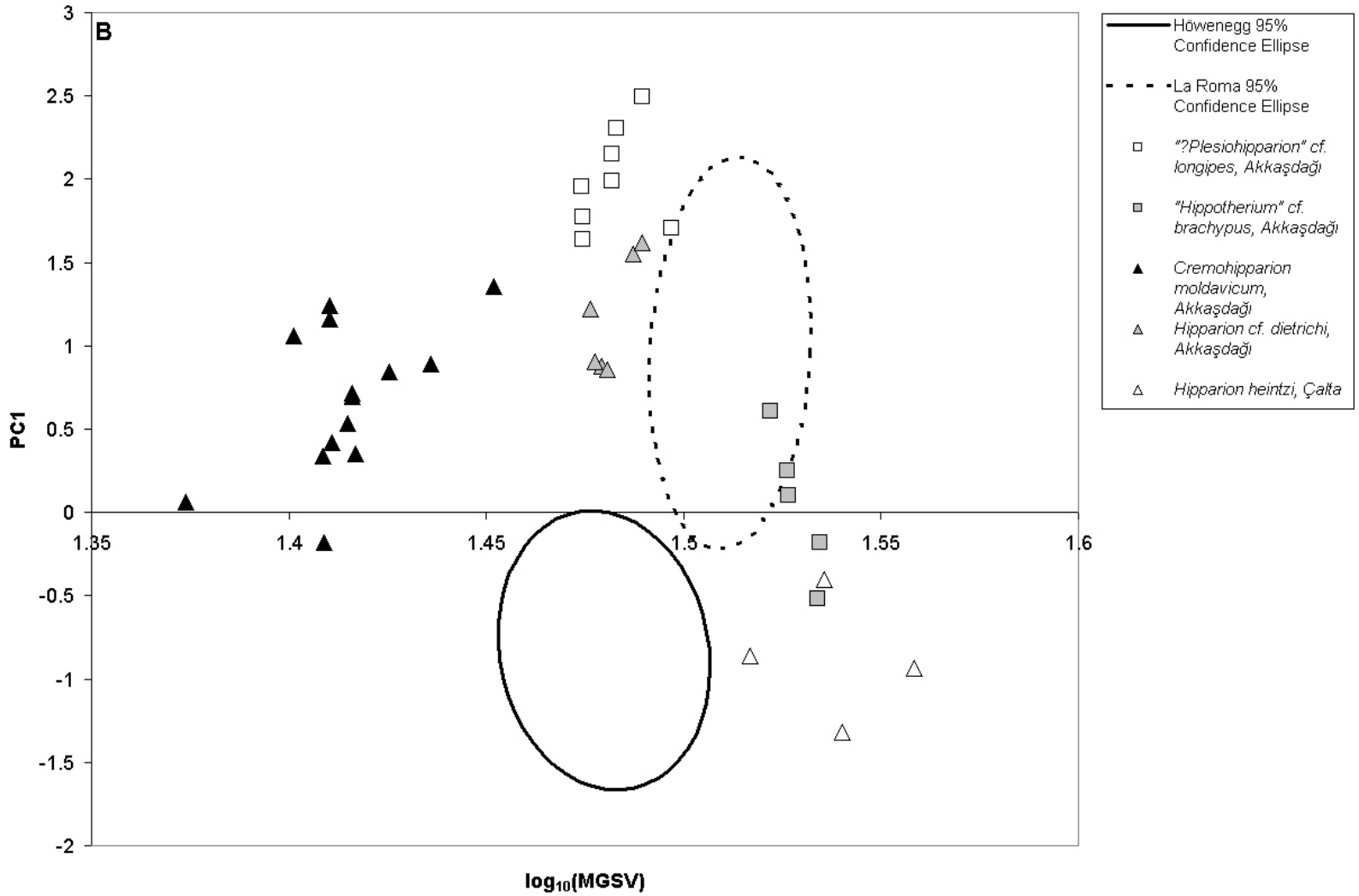


Figure 6.23: Plot of PC1 and $\log_{10}$(MGSV) for hipparionines from Akkaşdağı and Çalta. A, MT III's; B, MC III's. Specimens are shown by site and/or possible taxonomic identification and are plotted with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

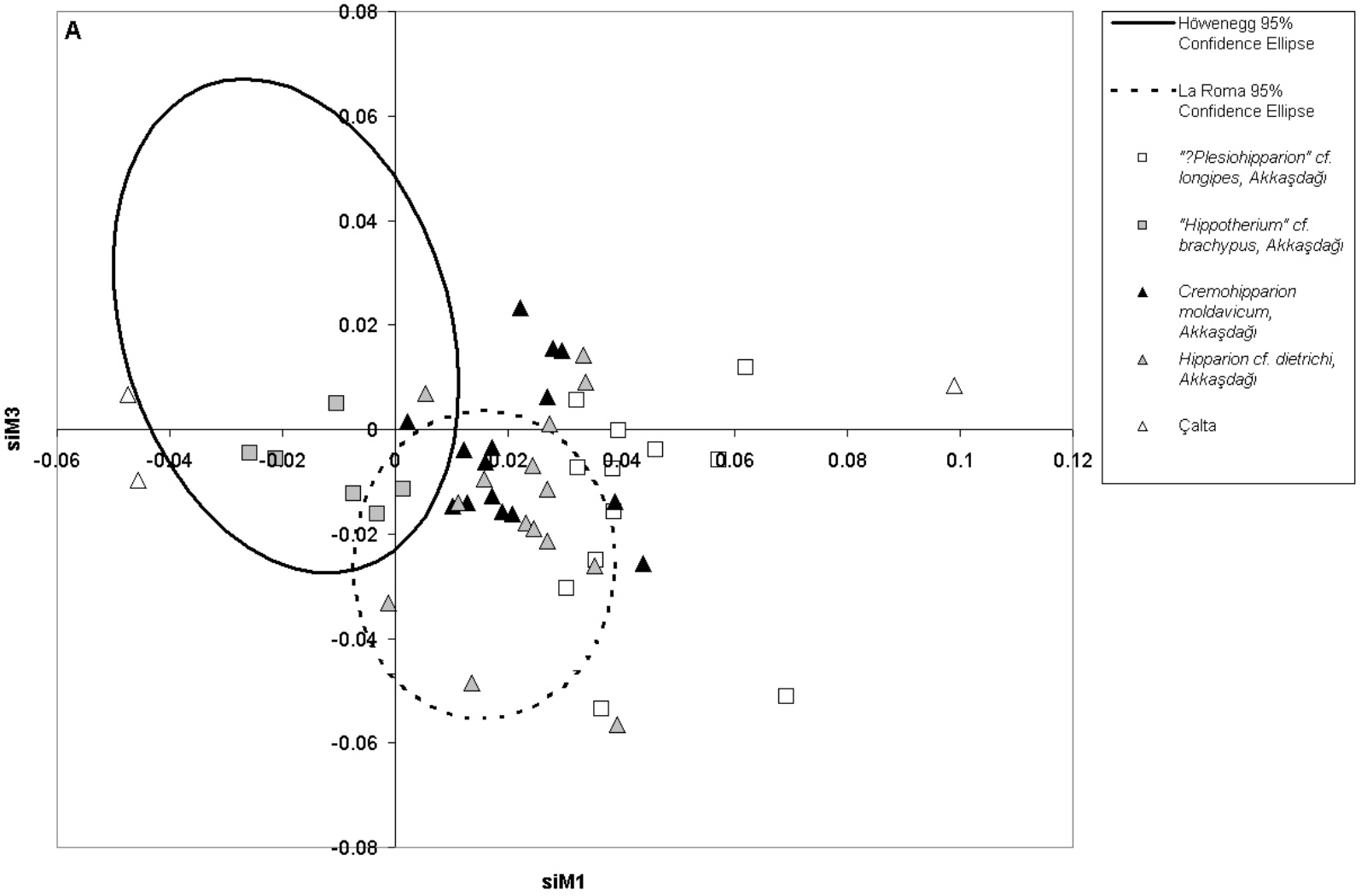


FIGURE 6.24: PLOT OF SIM3 AND SIM1 FOR HIPPARIONINES FROM AKKAŞDAĞI AND ÇALTA. A, MT III's; B, MC III's. Specimens are shown by site and/or possible taxonomic identification and are plotted with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

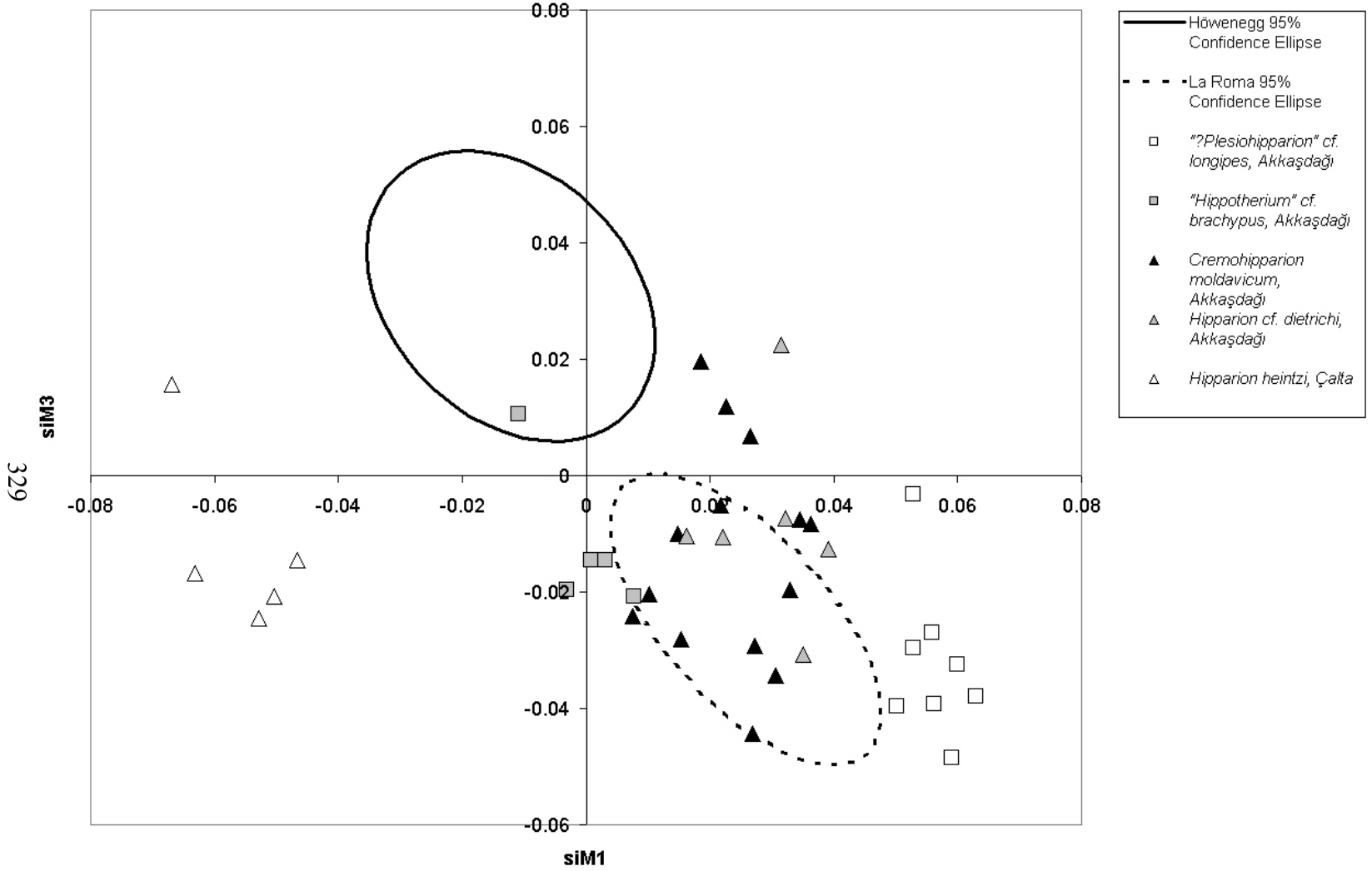


Figure 6.24: Plot of siM3 and siM1 for hipparionines from Akkaşdağı and Çalta. A, MT III's; B, MC III's. Specimens are shown by site and/or possible taxonomic identification and are plotted with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

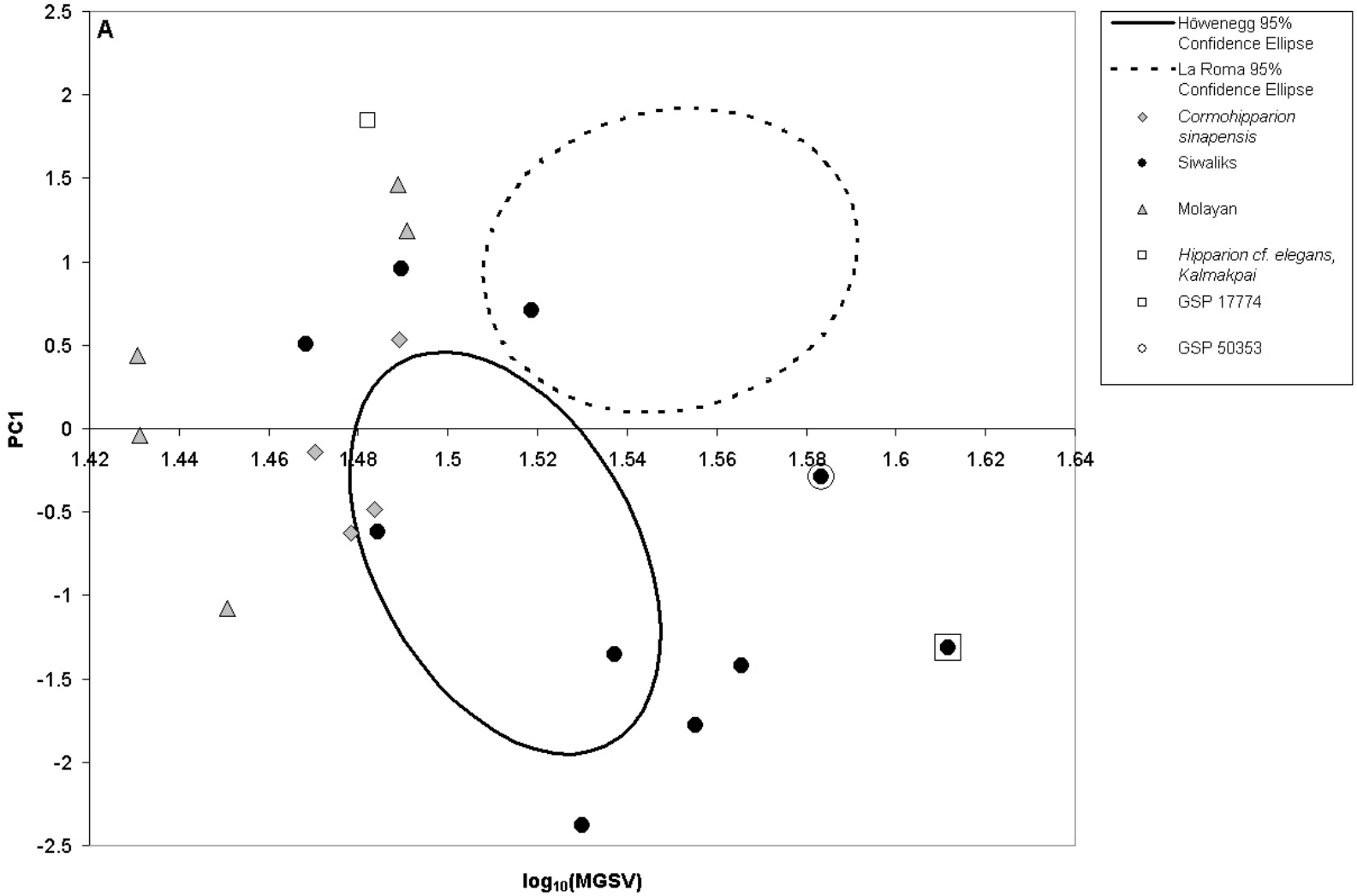


FIGURE 6.25: PLOT OF PC1 AND LOG10(MGSV) FOR HIPPARIONINES FROM KALMAKPAI, MOLAYAN, AND THE SIWALIKS. A, MT III's; B, MC III's. Specimens are shown by site and/or possible taxonomic identification and are plotted with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

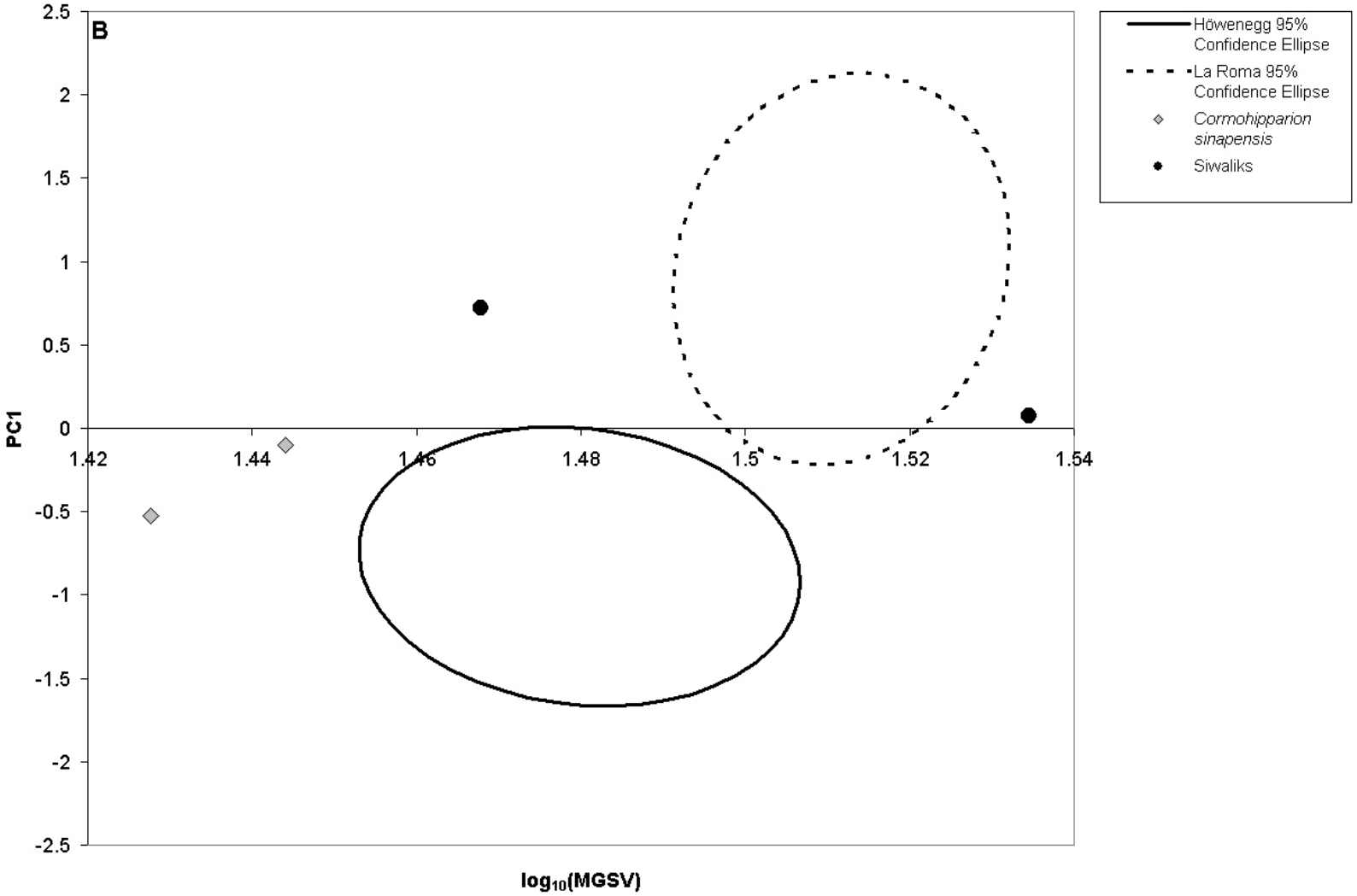


Figure 6.25: Plot of PC1 and $\log_{10}$(MGSV) for hipparionines from Kalmakpai, Molayan, and the Siwaliks. A, MT III's; B, MC III's. Specimens are shown by site and/or possible taxonomic identification and are plotted with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

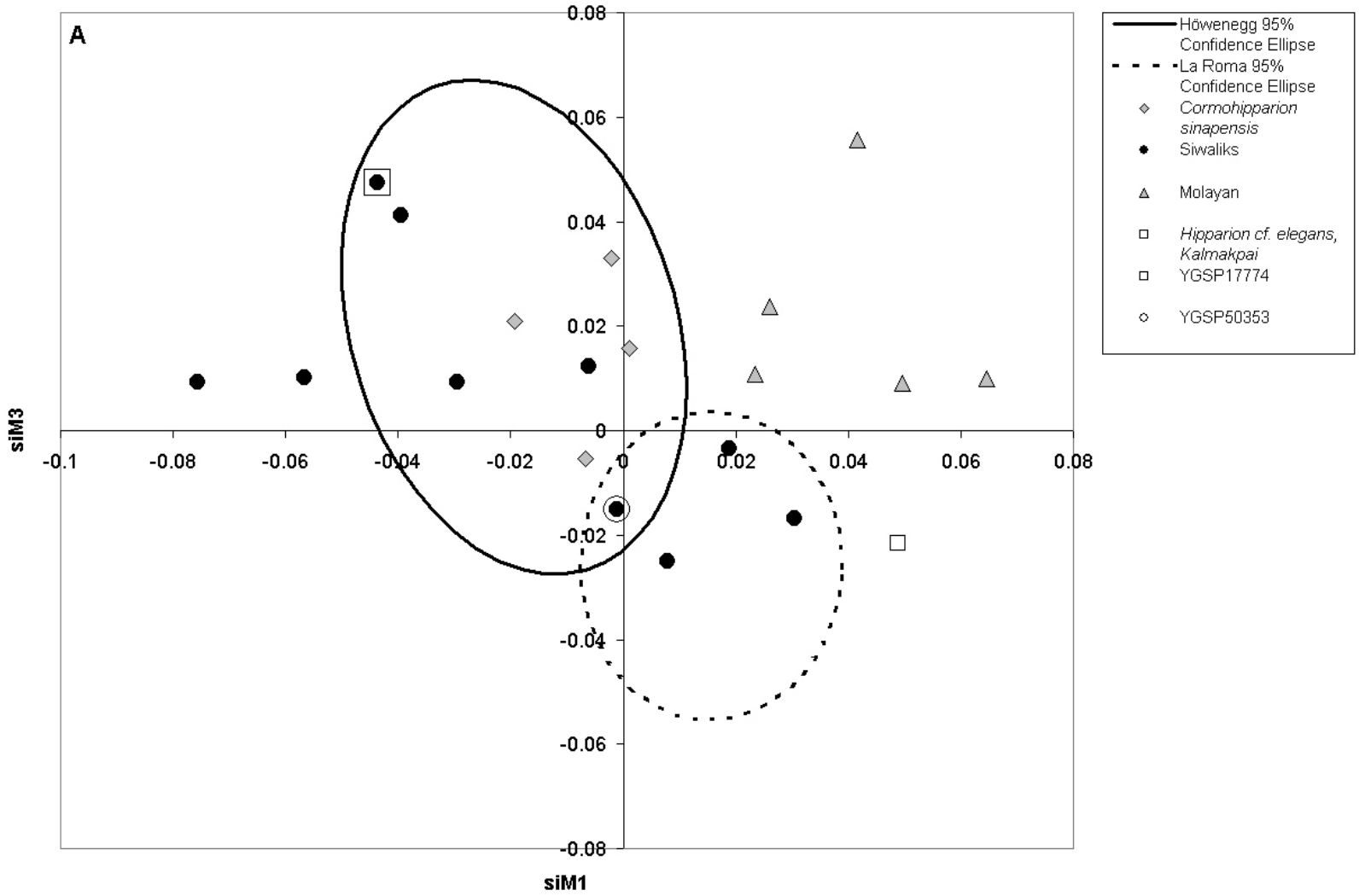


FIGURE 6.26: PLOT OF SIM3 AND SIM1 FOR HIPPARIONINES FROM KALMAKPAI, MOLAYAN, AND THE SIWALIKS. A, MT III's; B, MC III's. Specimens are shown by site and/or possible taxonomic identification and are plotted with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

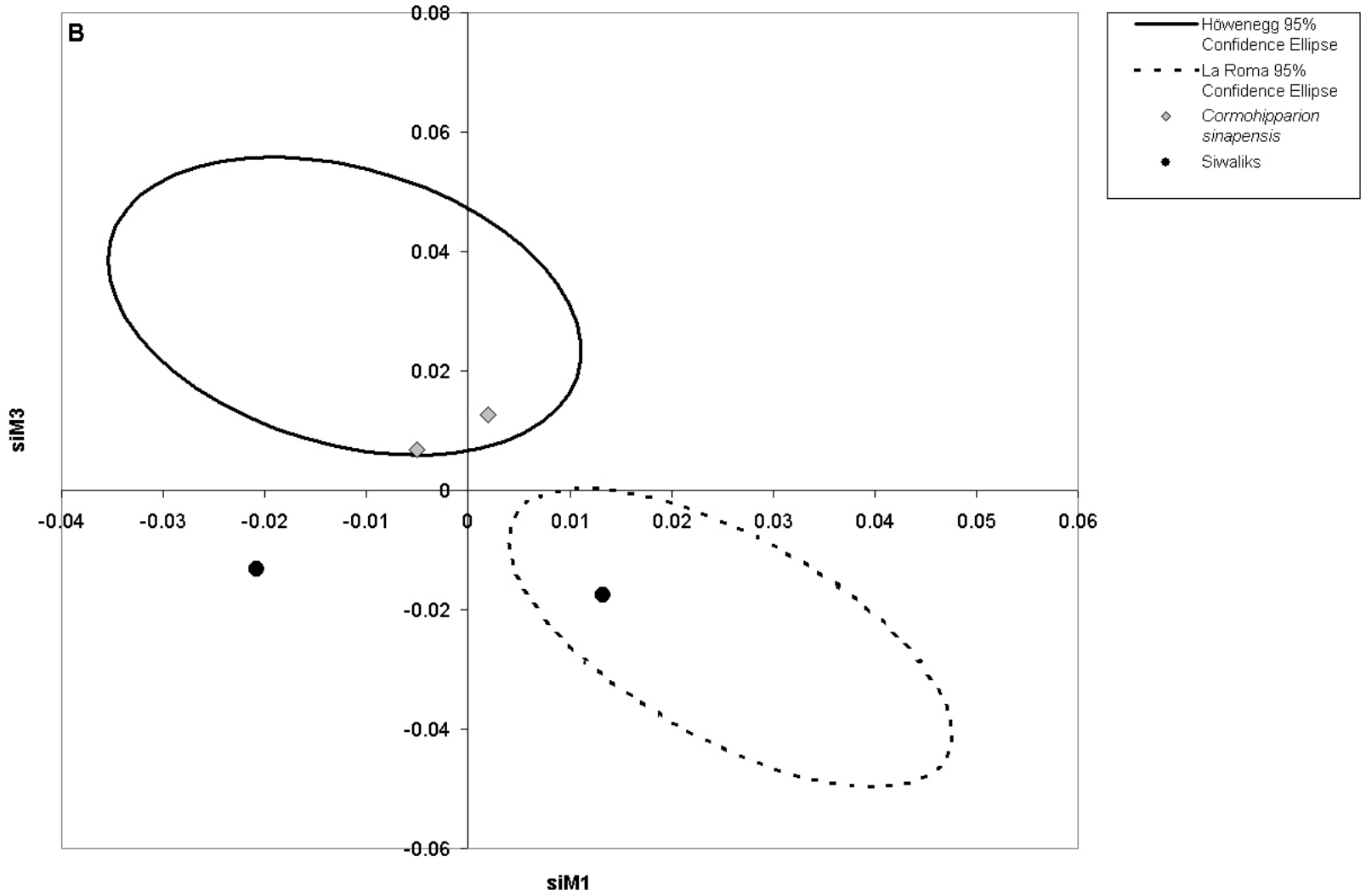


Figure 6.26: Plot of siM3 and siM1 for hipparionines from Kalmakpai, Molayan, and the Siwaliks. A, MT III's; B, MC III's. Specimens are shown by site and/or possible taxonomic identification and are plotted with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

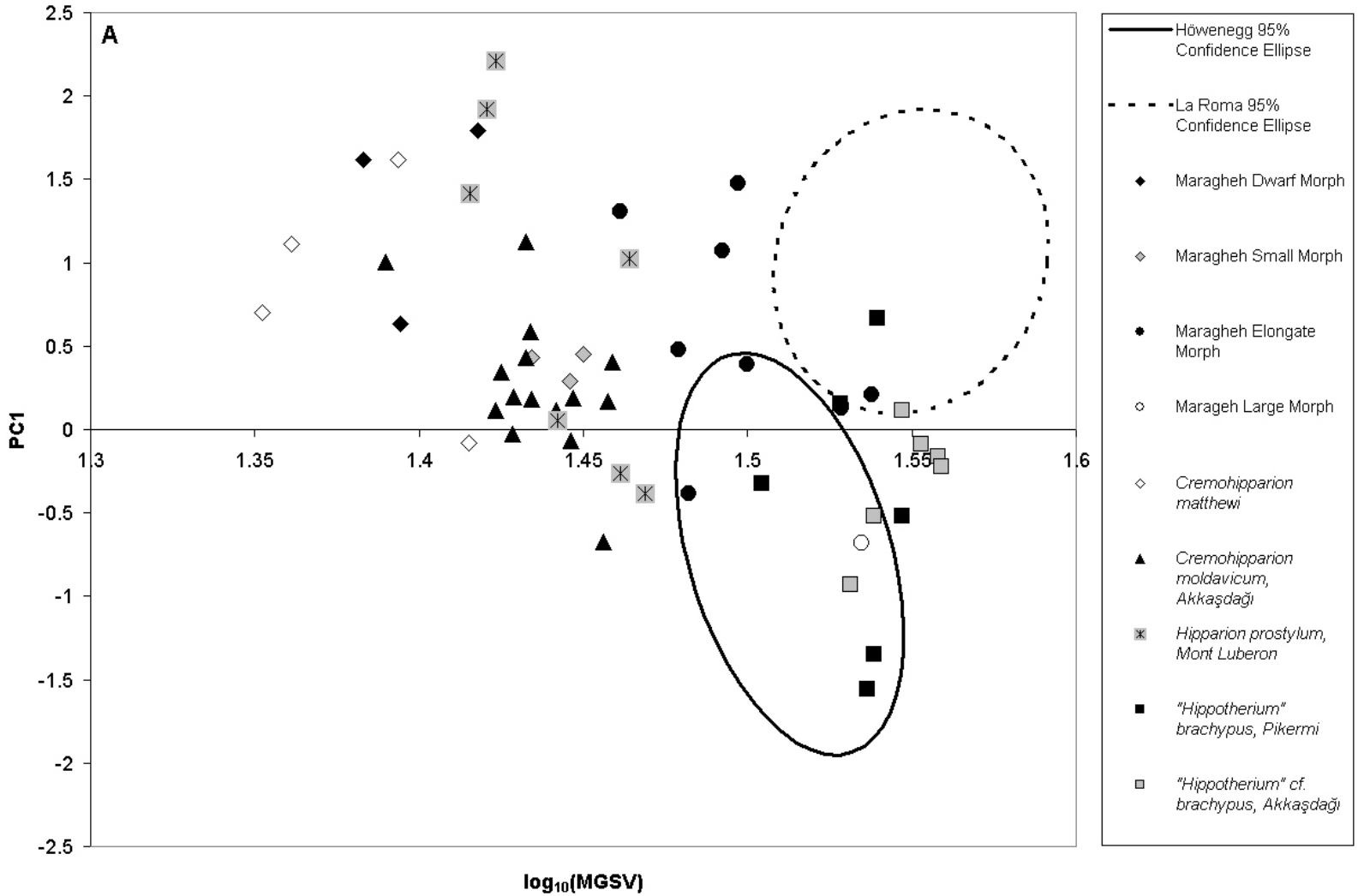


FIGURE 6.27: PLOT OF PC1 AND LOG10(MGSV) FOR HIPPARIONINES FROM MARAGHEH. A, MT III's; B, MC III's. Specimens are shown by morphological grouping (= Morph) and are plotted with selected comparisons and 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

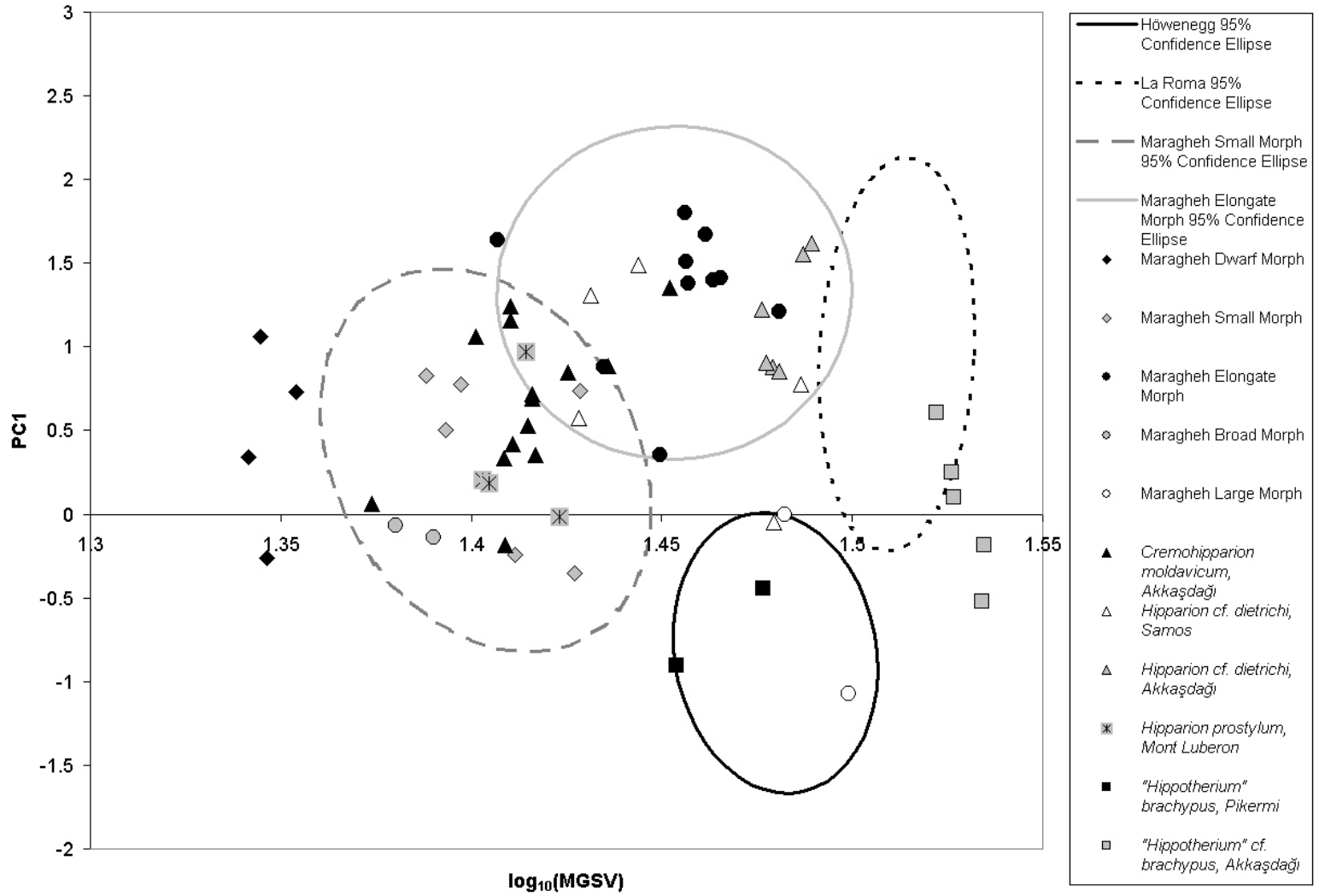


FIGURE 6.27: PLOT OF PC1 AND LOG10(MGSV) FOR HIPPARIONINES FROM MARAGHEH. A, MT III's; B, MC III's. Specimens are shown by morphological grouping (= Morph) and are plotted with selected comparisons and 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

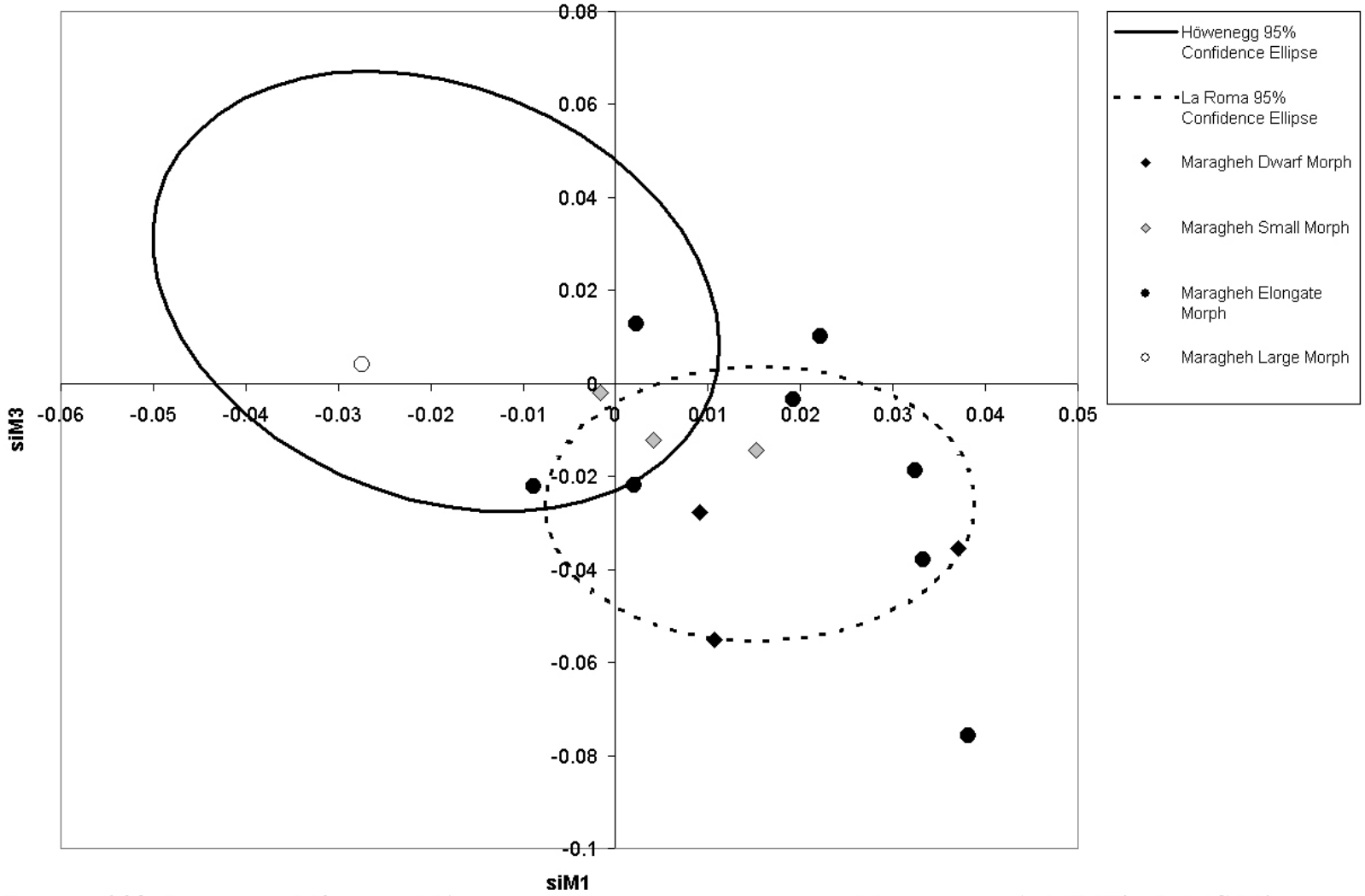


FIGURE 6.28: PLOT OF SIM3 AND SIM1 FOR HIPPARIONINES FROM FROM MARAGHEH. A, MT III's; B, MC III's. Specimens are shown by morphological grouping (= Morph) and are plotted with selected comparisons and 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

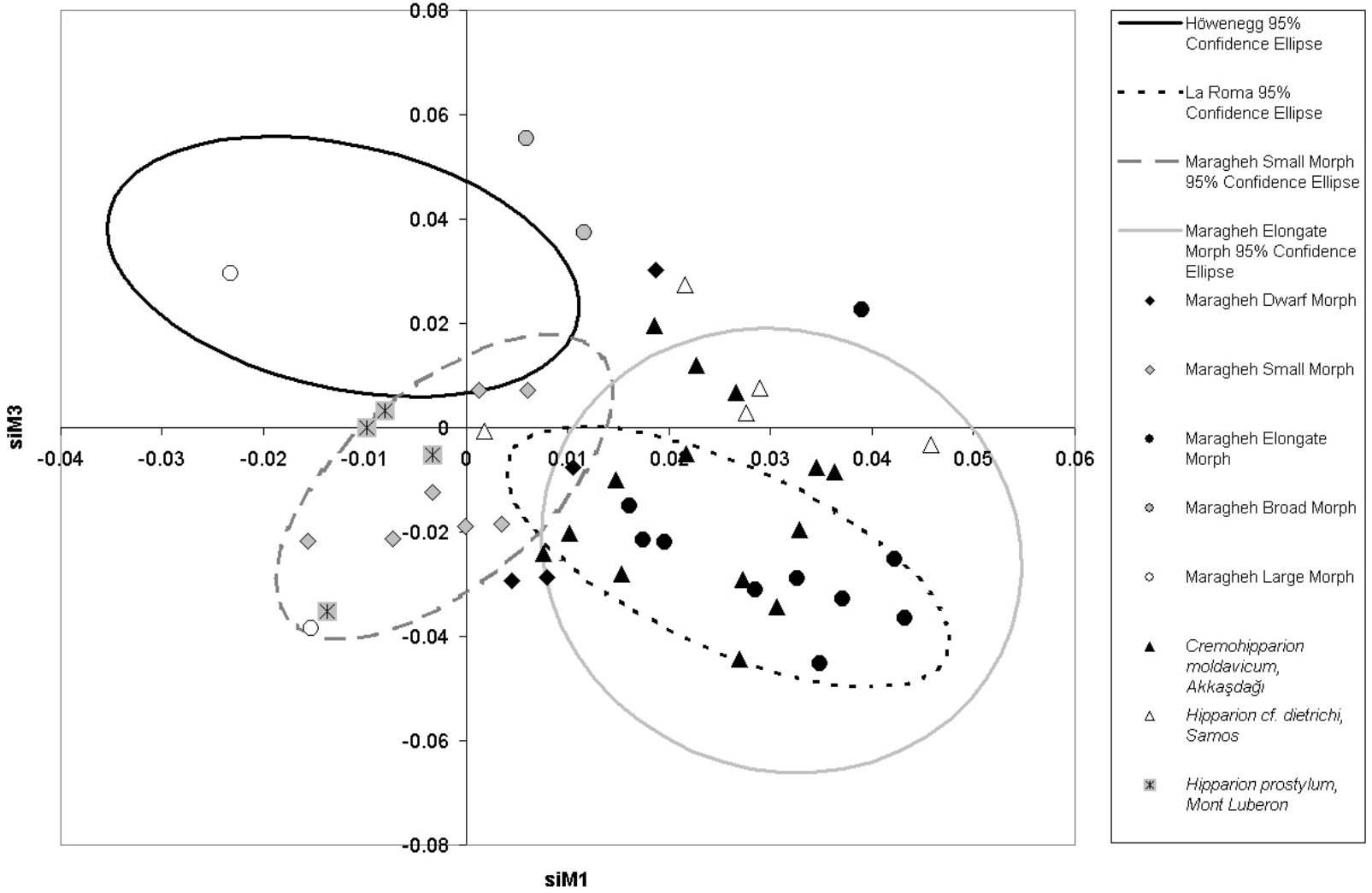


FIGURE 6.28: PLOT OF SIM3 AND SIM1 FOR HIPPARIONINES FROM FROM MARAGHEH. A, MT III's; B, MC III's. Specimens are shown by morphological grouping (= Morph) and are plotted with selected comparisons and 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

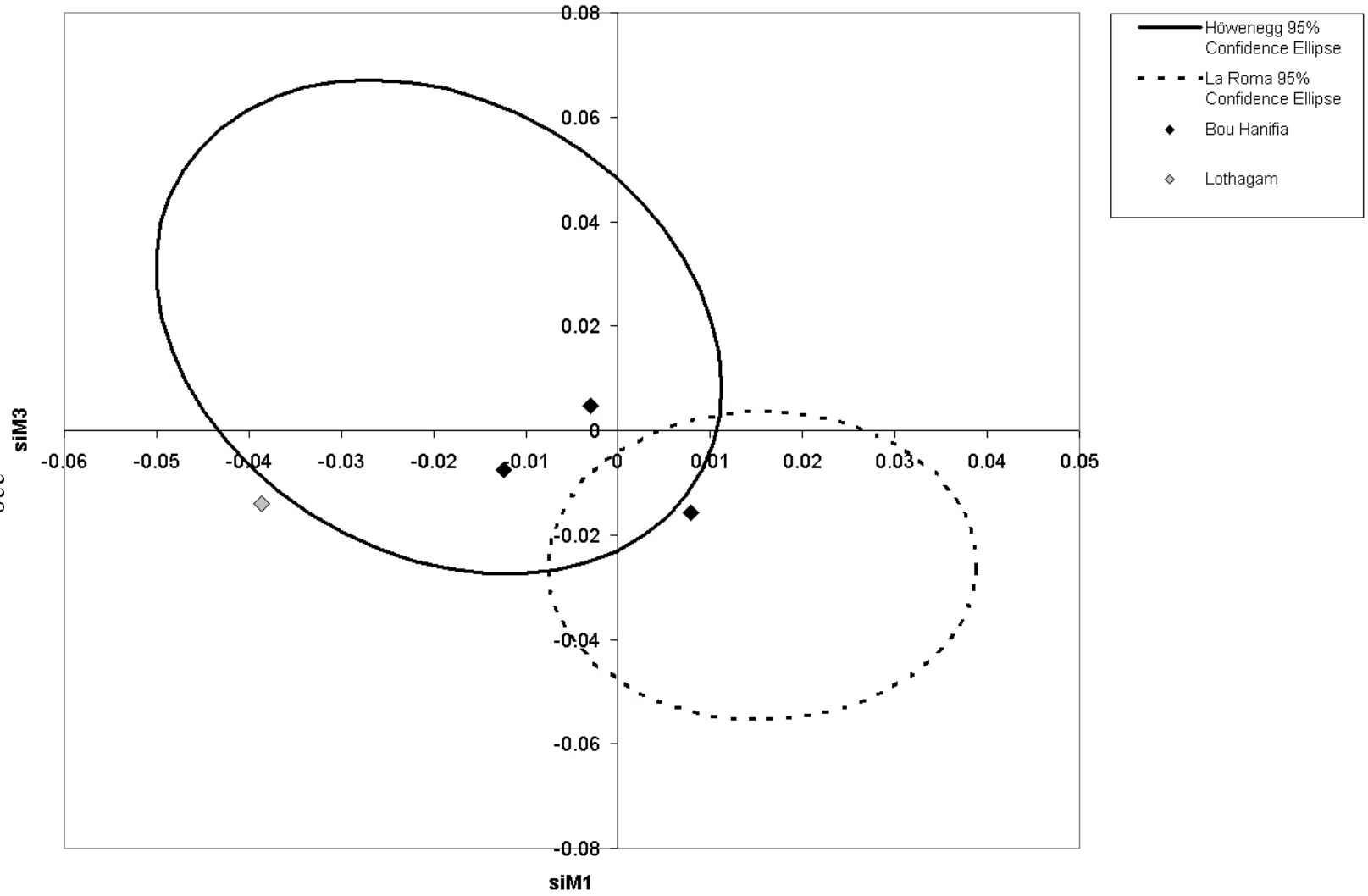


Figure 6.29: Plot of siM3 and siM1 for hipparionines from from Africa. A, MT III's; B, MC III's. Specimens are shown by site and are plotted with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

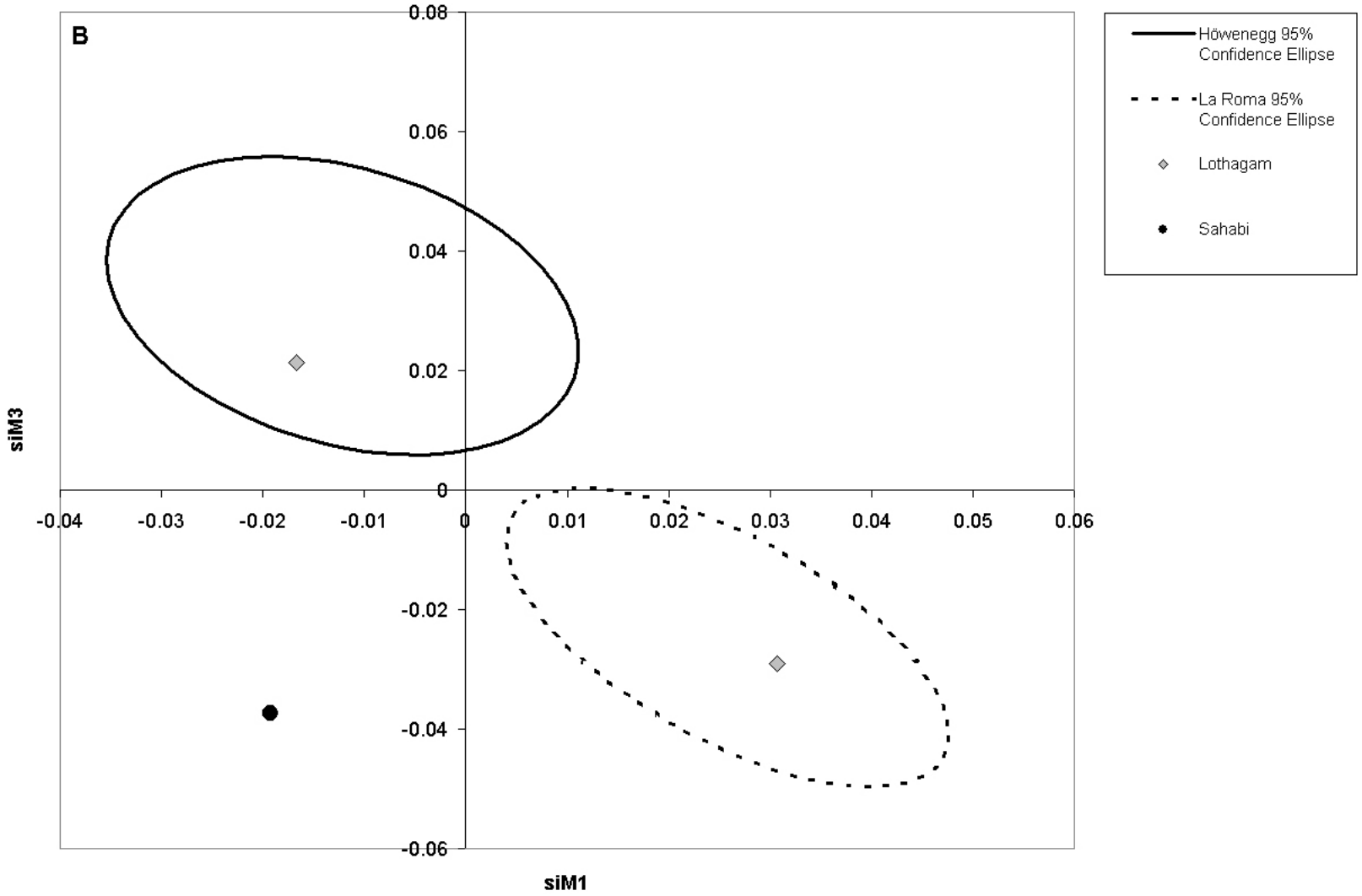


Figure 6.29: Plot of siM3 and siM1 for hipparionines from from Africa. A, MT III's; B, MC III's. Specimens are shown by site and are plotted with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

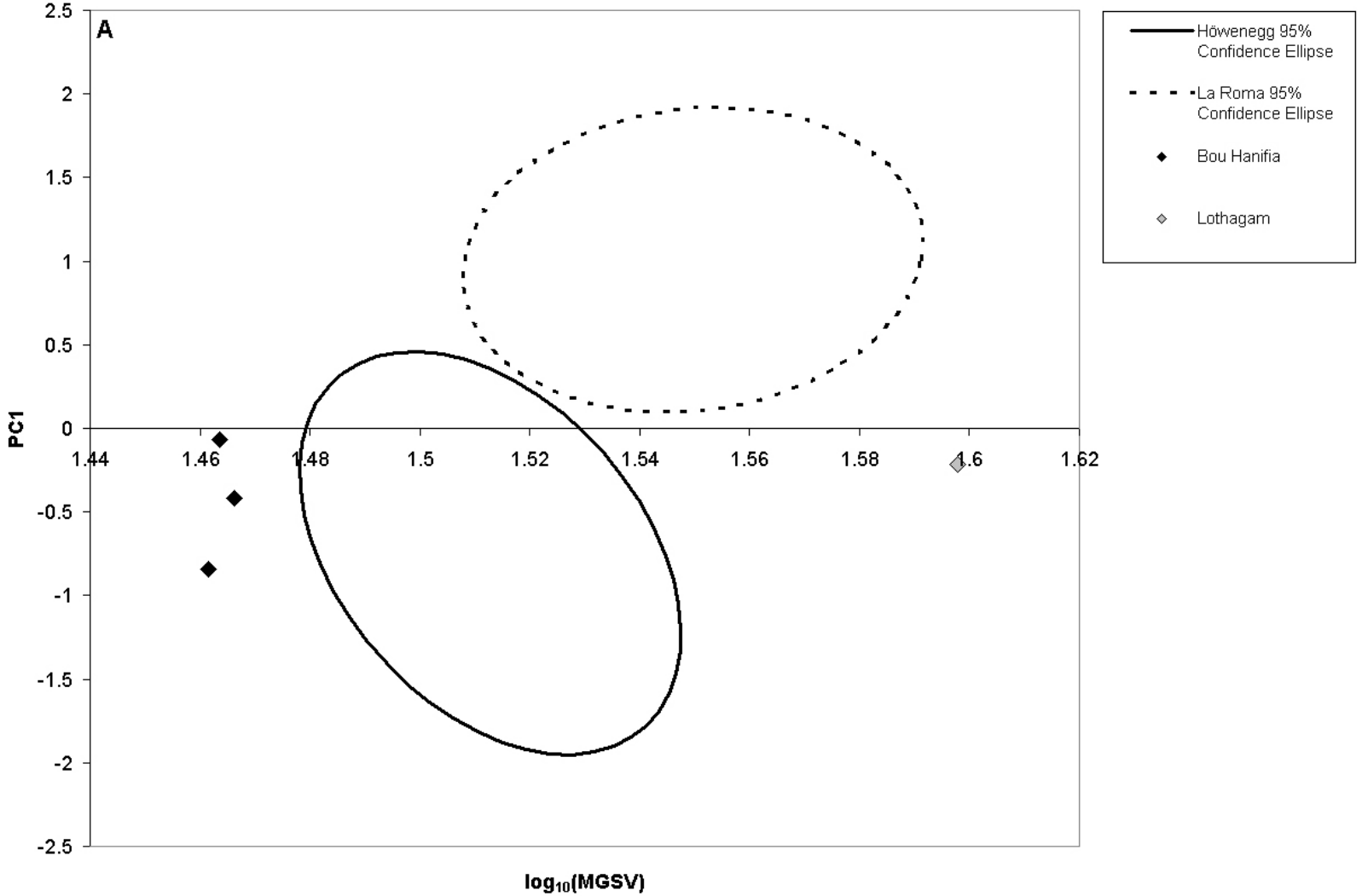


Figure 6.30: Plot of PC1 and $\log_{10}$(MGSV) for hipparionines from Africa. A, MT III's; B, MC III's. Specimens are shown by site and are plotted with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

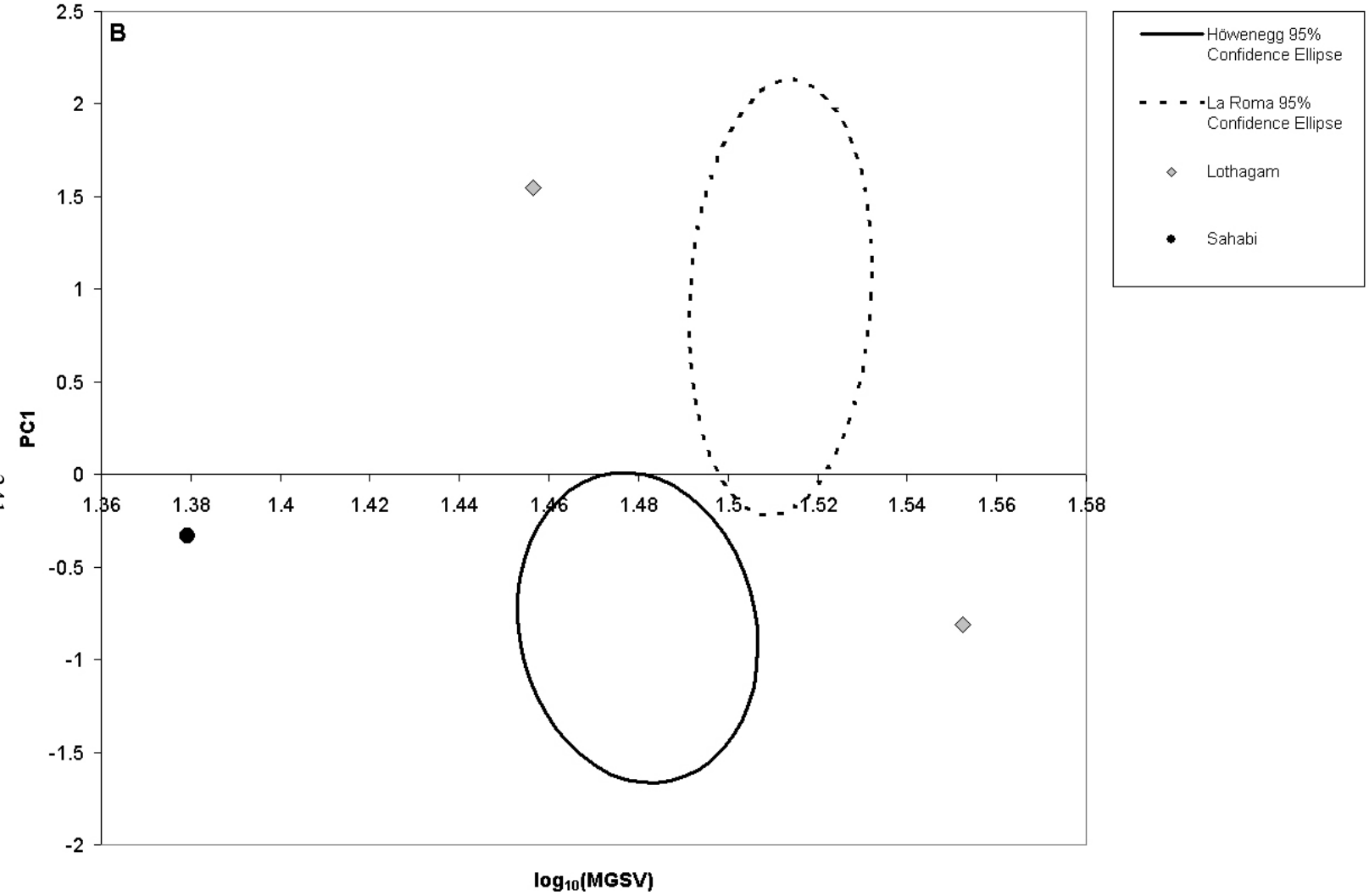


Figure 6.30: Plot of PC1 and $\log_{10}$(MGSV) for hipparionines from Africa. A, MT III's; B, MC III's. Specimens are shown by site and are plotted with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

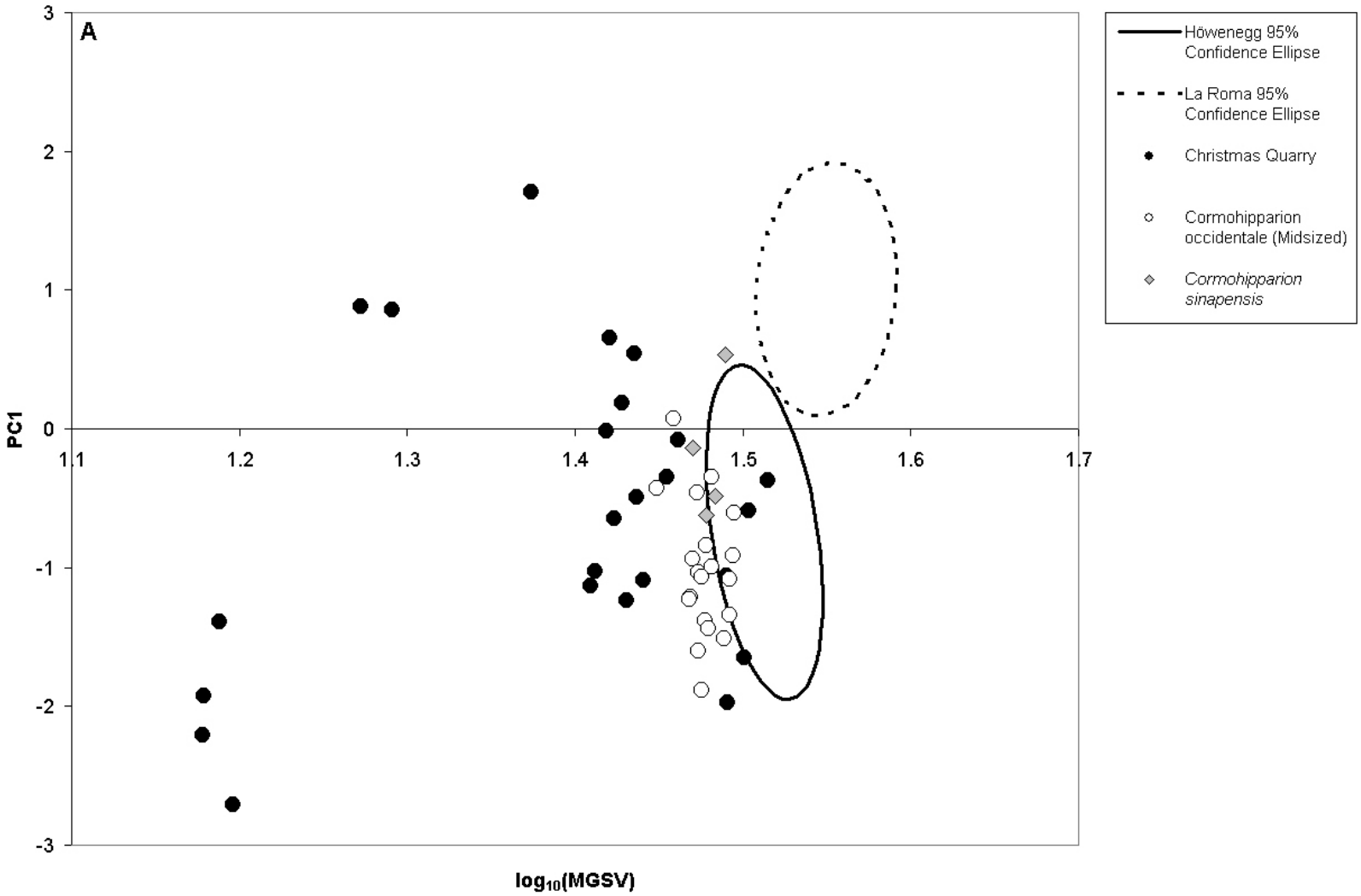


Figure 6.31: Plot of PC1 and $\log_{10}$(MGSV) for hipparionines from Christmas Quarry and *Cormohipparion sinapensis*. A, MT III's; B, MC III's. Specimens are shown by site and are plotted with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

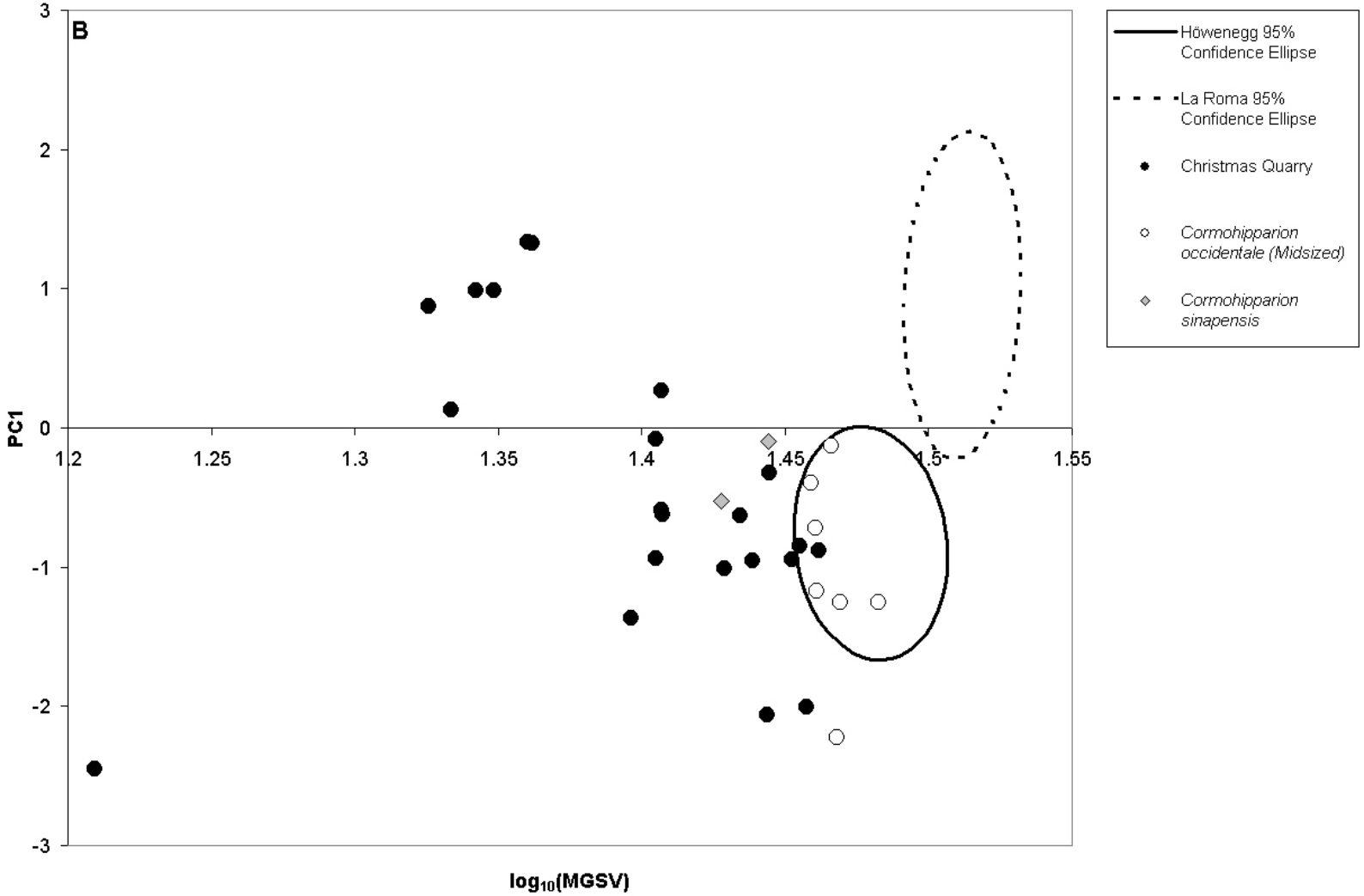


Figure 6.31: Plot of PC1 and $\log_{10}$(MGSV) for hipparionines from Christmas Quarry and *Cormohipparion sinapensis*. A, MT III's; B, MC III's. Specimens are shown by site and are plotted with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

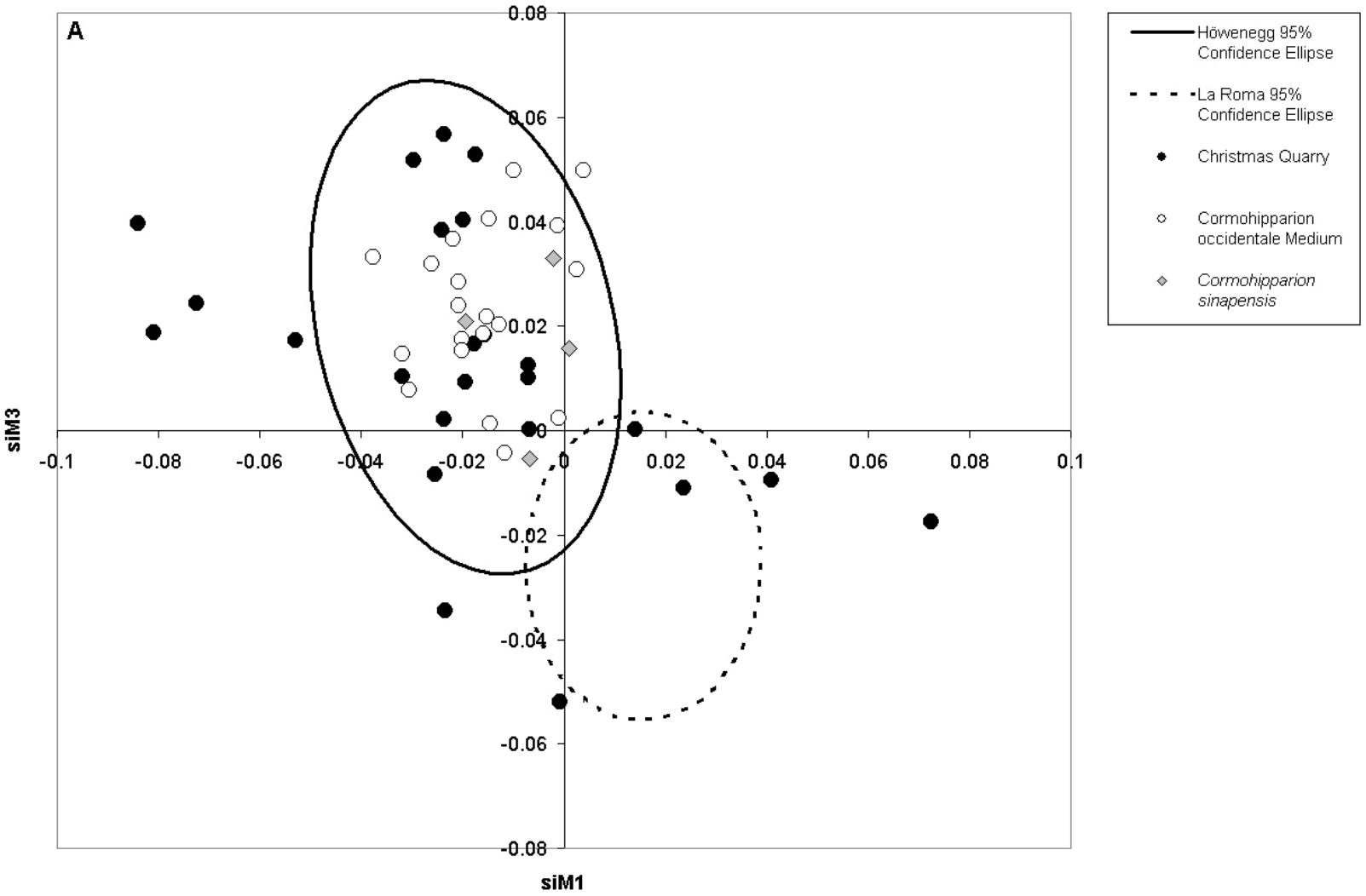


Figure 6.32: Plot of siM3 and siM1 for hipparionines from Christmas Quarry and *Cormohipparion sinapensis*. A, MT III's; B, MC III's. Specimens are shown by site and are plotted with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

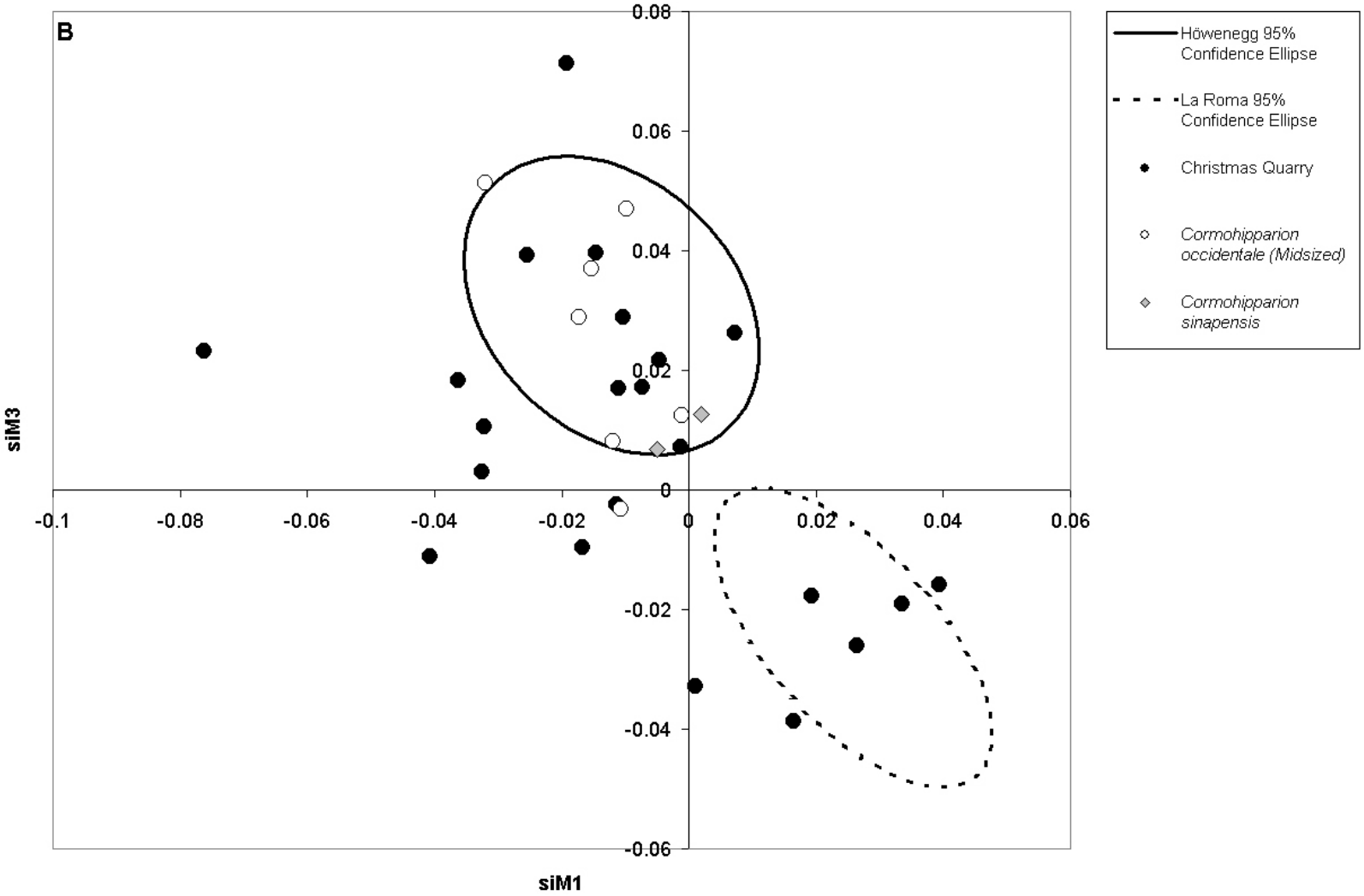


Figure 6.32: Plot of siM3 and siM1 for hipparionines from Christmas Quarry and *Cormohipparion sinapensis*. A, MT III's; B, MC III's. Specimens are shown by site and are plotted with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

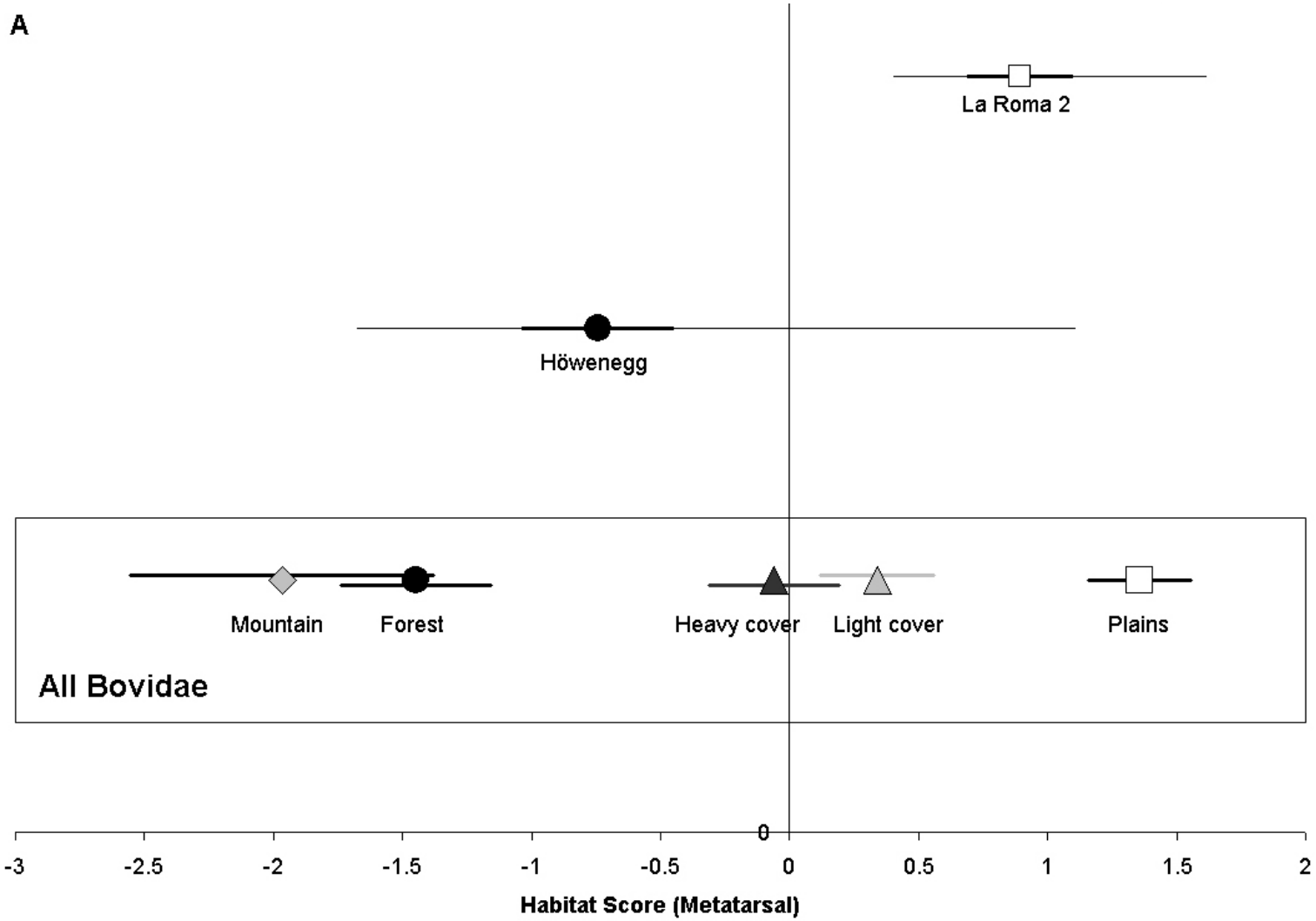


Figure 6.33: Summary plot of habitat scores for the Höwenegg and La Roma 2 standards. A, MT III's; B, MC III's. The horizontal axis is habitat score (based on size, metapodial length, and metapodial width at midshaft) .

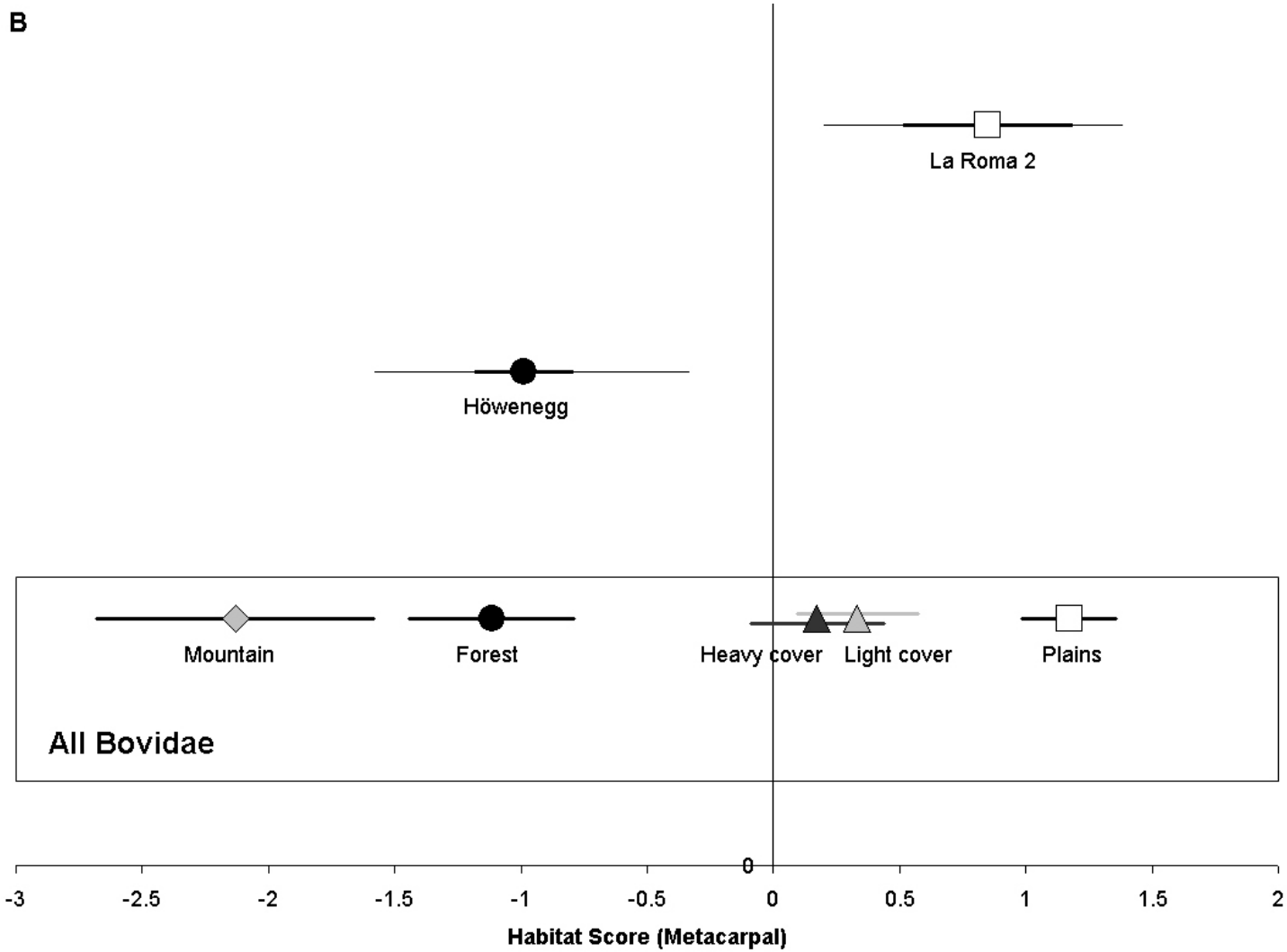


Figure 6.33: Summary plot of habitat scores for the Höwenegg and La Roma 2 standards. A, MT III's; B, MC III's. The horizontal axis is habitat score (based on size, metapodial length, and metapodial width at midshaft) .

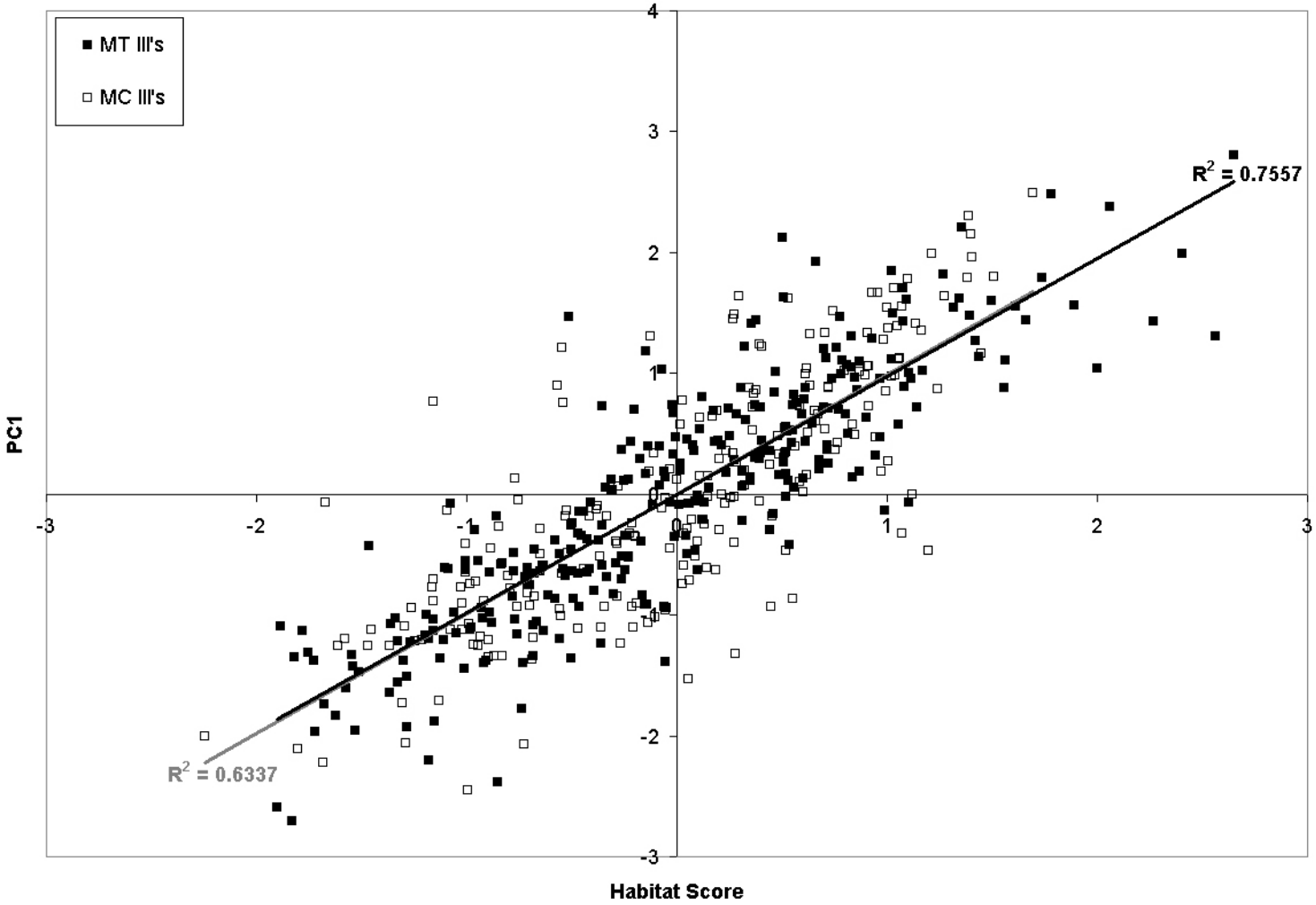


Figure 6.34: Least squares regression of PC1 versus habitat score. PC1 is plotted and regressed versus habitat score for the complete sample of hipparionines. MT III's are shown as filled squares (■) and MC III's are shown as open squares (□). III's. The complete hipparionine sample is shown by habitat group with the best fit least squares regression line for $\log_{10}$(MLEN) versus $\log_{10}$(MGSV). R^2 for MT III's is shown at the upper right and R^2 for MC III's is shown at the lower left.

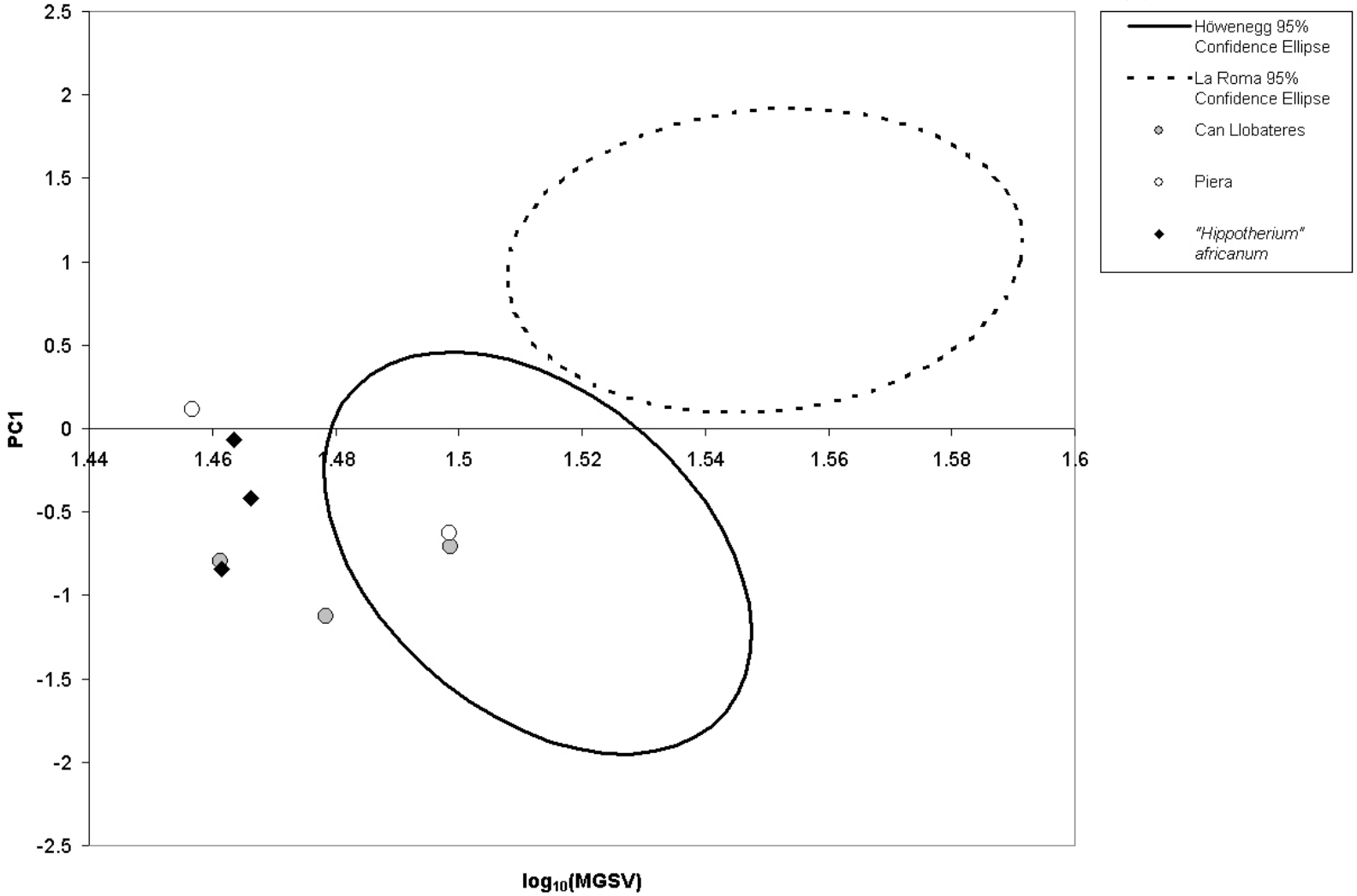


Figure 6.35: Plot of PC1 and $\log_{10}$(MGSV) for MT III's of a possible *"Hippotherium" catalaunicum-africanum* clade. Specimens are shown by site and/or possible taxonomic identification and are plotted with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

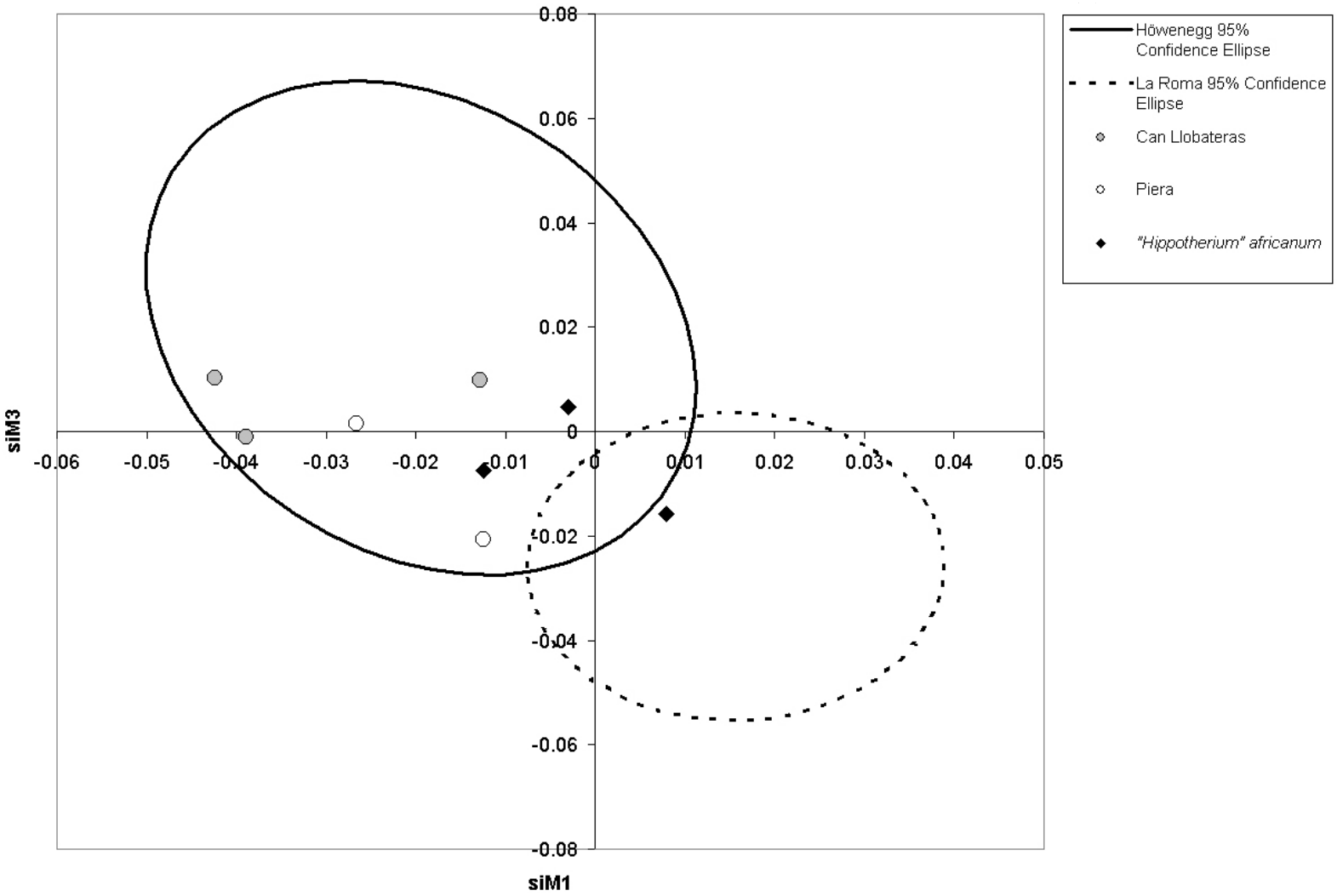


Figure 6.36: Plot of siM3 and siM1 for MT III's of a possible *"Hippotherium" catalaunicum-africanum* clade. Specimens are shown by site and/or possible taxonomic identification and are plotted with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

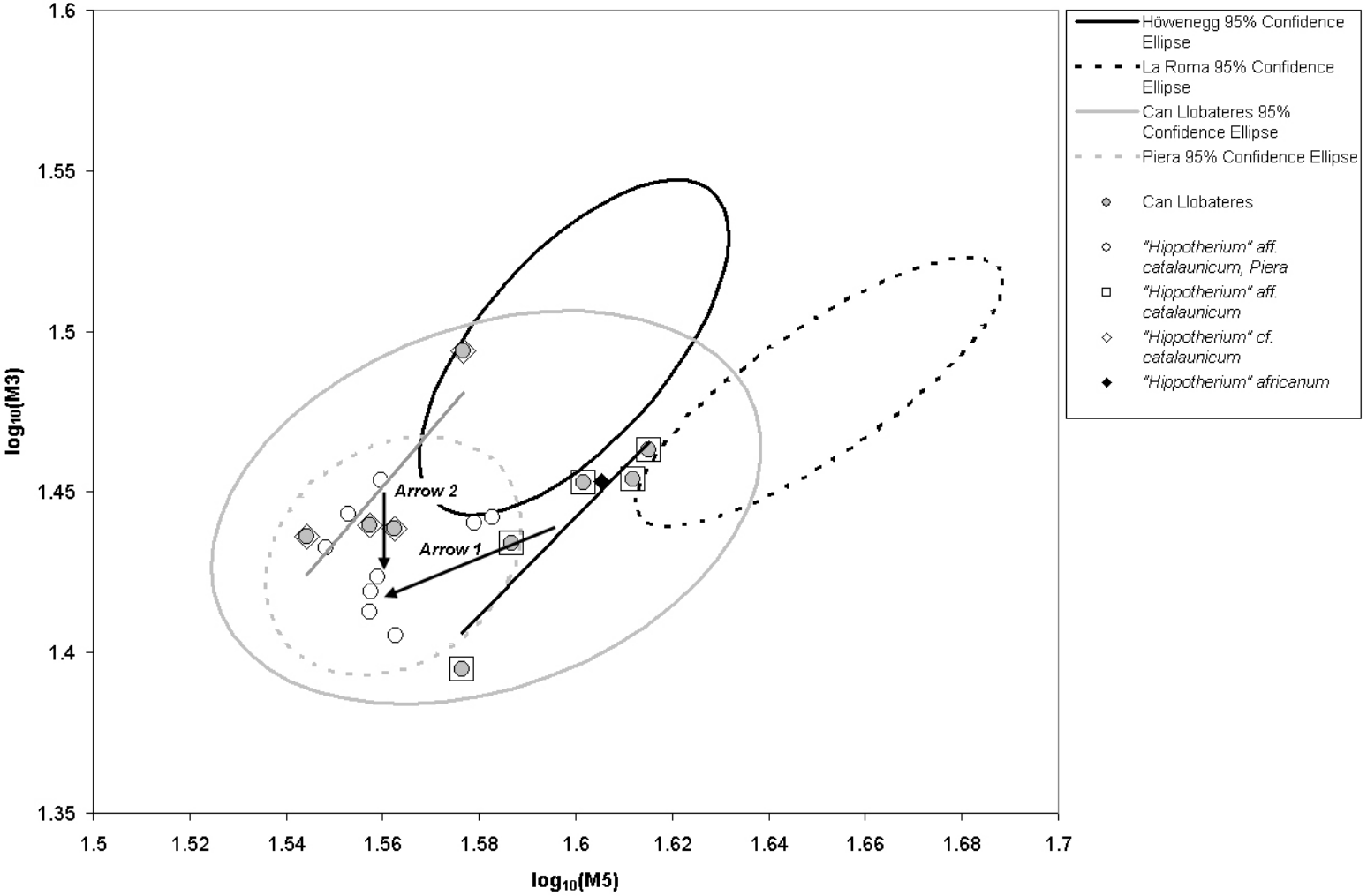


Figure 6.37: Plot of $\log_{10}$(M3) and $\log_{10}$(M5) for MC III's of a possible *"Hippotherium" catalaunicum-africanum* clade. MC III's from Can Llobateres are divided into two possible species with separate best fit least squares regression lines. Specimens are shown by site and/or possible taxonomic identification and are plotted with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

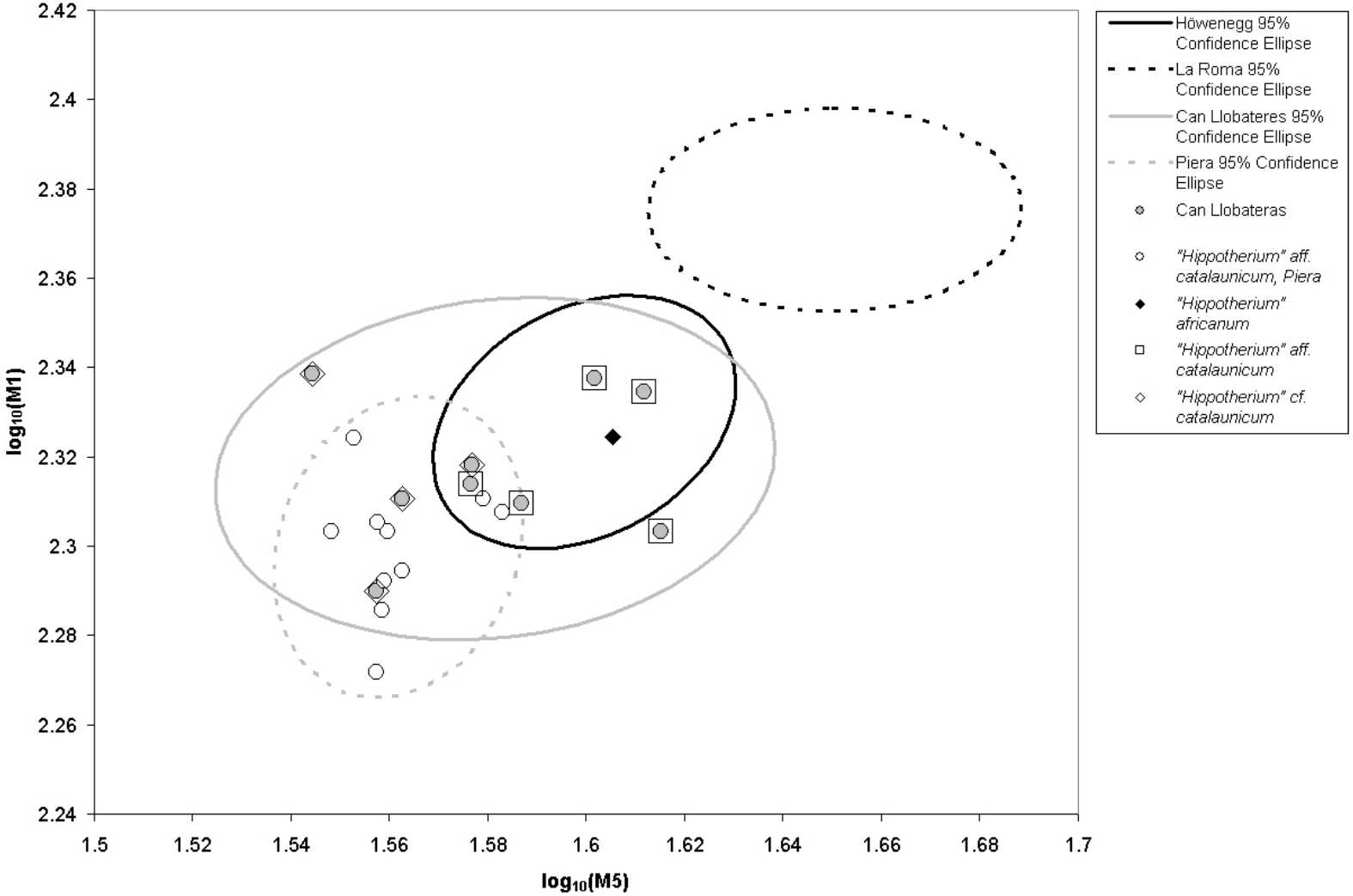
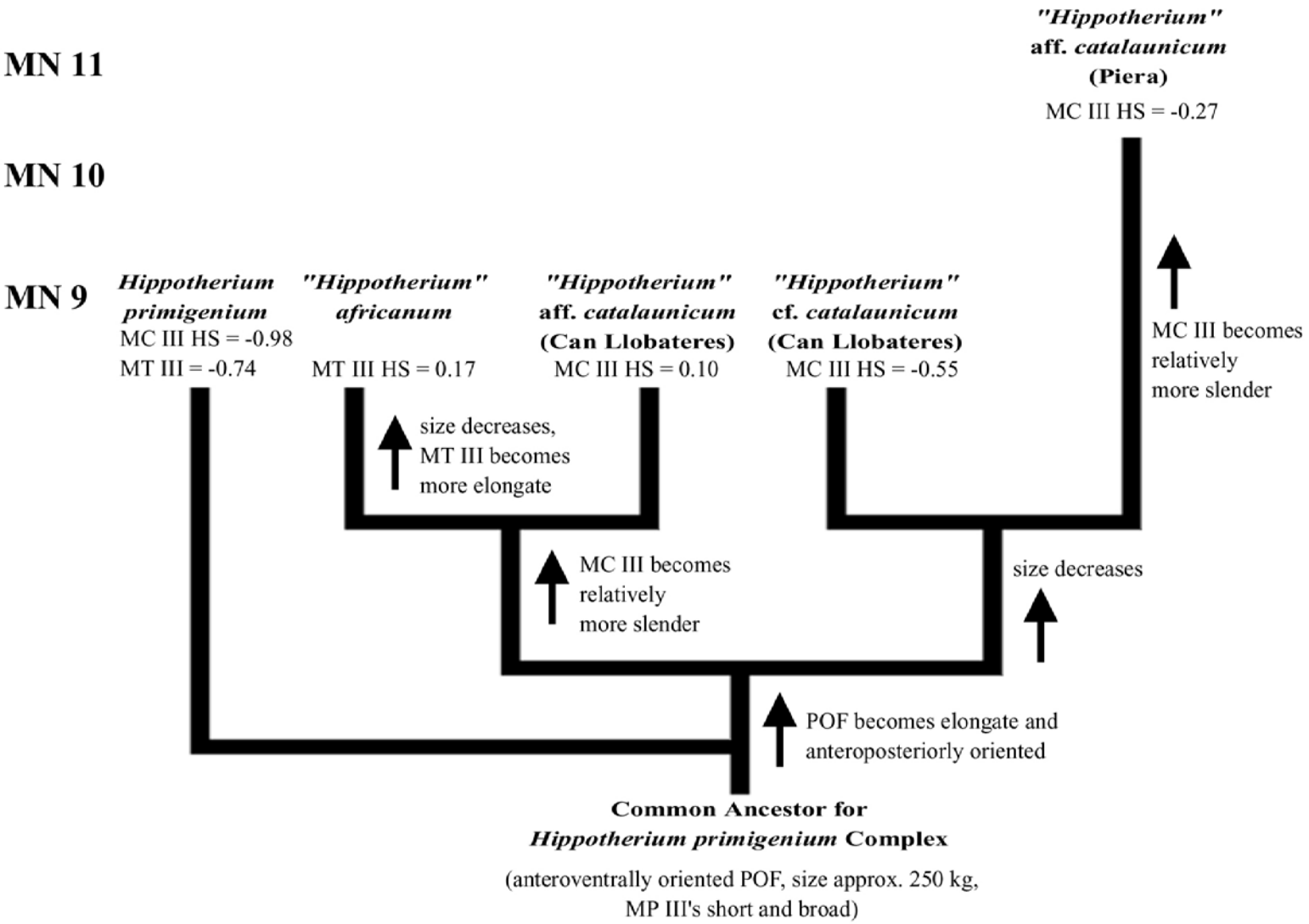


Figure 6.38: Plot of $\log_{10}$(M1) and $\log_{10}$(M5) for MC III's of a possible *"Hippotherium" catalaunicum-africanum* clade. MC III's from Can Llobateres are divided into two possible species. Specimens are shown by site and/or possible taxonomic identification and are plotted with 95% confidence ellipses for the Höwenegg and La Roma 2 standards.


MN 11
MN 10
MN 9
"Hippotherium"
aff. catalaunicum
(Piera)
MC III HS = -0.27
Hippotherium
primigenium
MC III HS = -0.98
MT III = -0.74
"Hippotherium"
africanum
MT III HS = 0.17
"Hippotherium"
aff. catalaunicum
(Can Llobateres)
MC III HS = 0.10
"Hippotherium"
cf. catalaunicum
(Can Llobateres)
MC III HS = -0.55
MC III becomes
relatively
more slender
size decreases,
MT III becomes
more elongate
MC III becomes
relatively
more slender
size decreases
POF becomes elongate and
anteroposteriorly oriented
Common Ancestor for
Hippotherium primigenium Complex
(anteroventrally oriented POF, size approx. 250 kg,
MP III's short and broad)

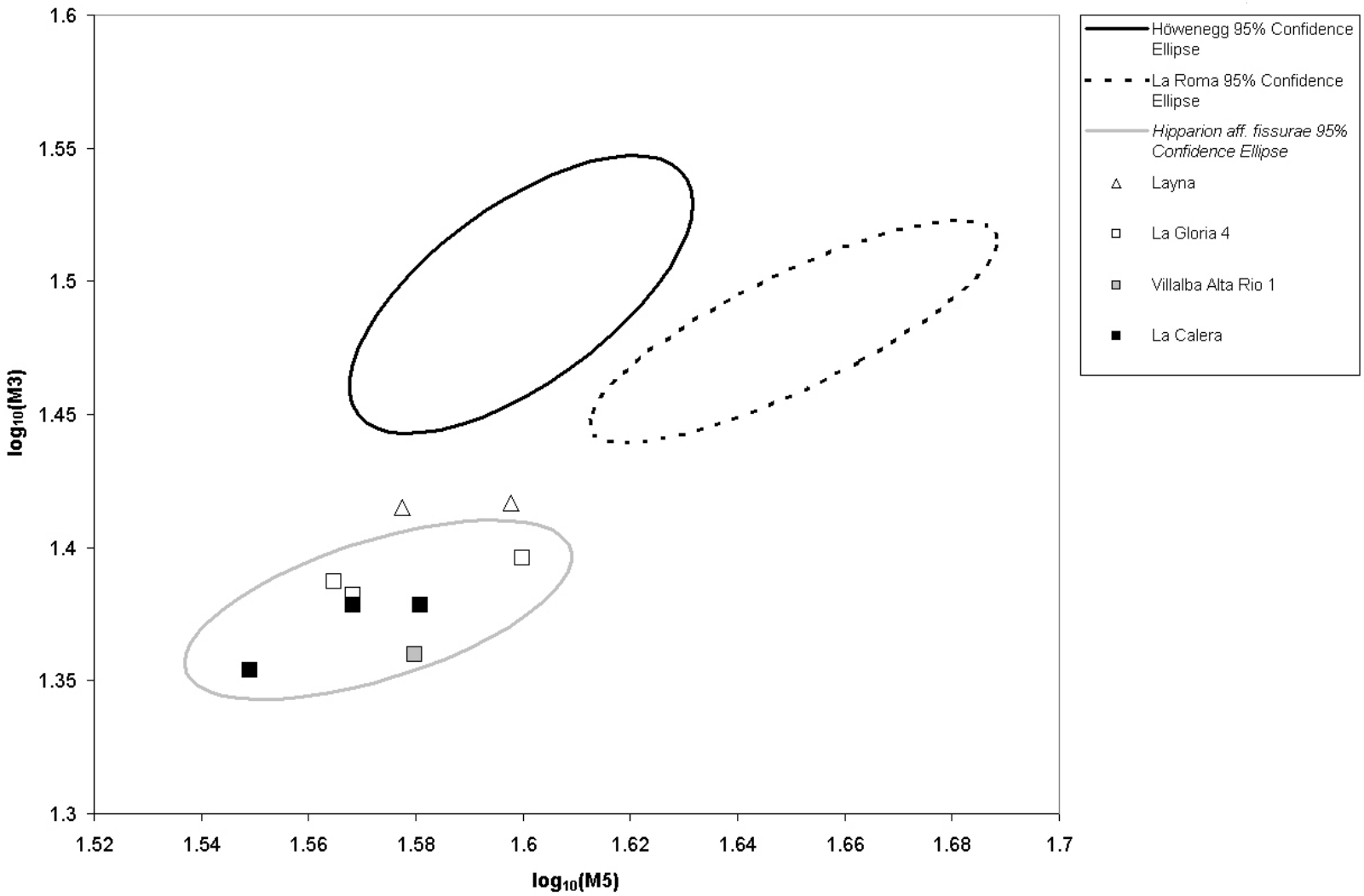


Figure 6.40: Plot of $\log_{10}$(M3) and $\log_{10}$(M5) for MC III's from Layna compared with *Hipparion* aff. *fissurae*. MC III's from Layna (Soria, Spain) are plotted with MC III's attributed to Hipparion aff. fissurae from La Gloria 4, Villalba Alta Rio 1, and La Calera. Measurements are from Alberdi and Alcalá (1999.

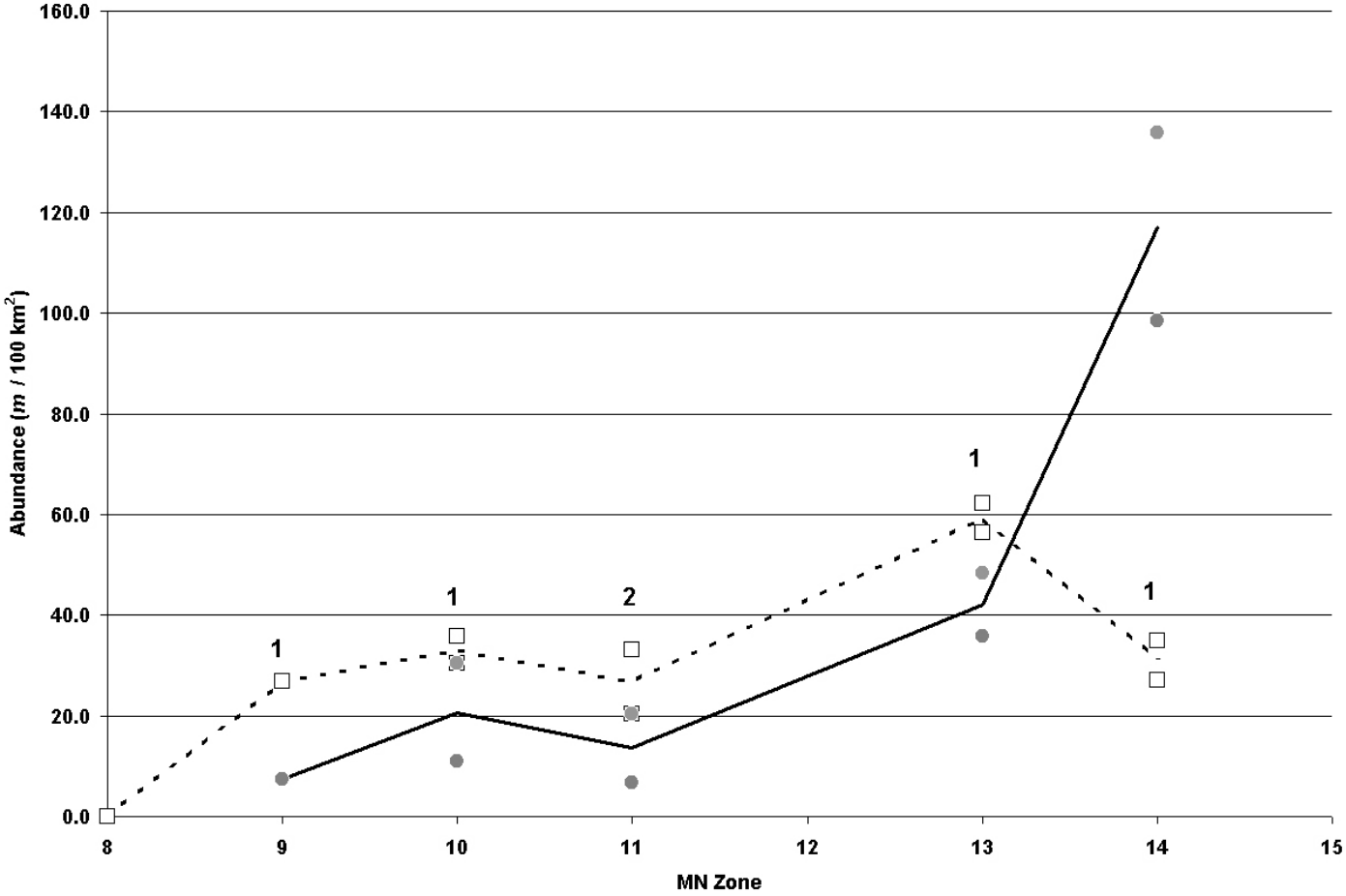


Figure 6.41: Plot of MNI- and NISP-based estimates of hipparionine and ruminant abundance at Los Valles de Fuentidueña and Teruel area localities. The model outlined by Scott et al. (2003) was applied with an assumption of constant ruminant plus hipparion biomass to published MNI's and NISP's for Teruel localities (Alcalá, 1994)and Los Valles de Fuentidueña (Alberdi, 1981; Morales and Soria, 1981) to provide abundance estimates for hipparionines and ruminants at these localities. Abundance is expressed in the units *m*/100 km^2 (see Scott et al., 2003) and plotted as open squares (□)and a dashed line for hipparionines and as lightly filled circles (●)and a solid line for ruminants. The horizontal axis corresponds to MN zone and each MN zone is represented by a single locality: MN 9 = Los Valles de Fuentidueña, MN 10 = La Roma 2, MN 11 = Puente Minero, MN 13 = Milagros, and MN 14 = La Gloria 4. Estimated hipparionine species diversity is denoted by numbers above the abundance data points for each MN zone / locality.

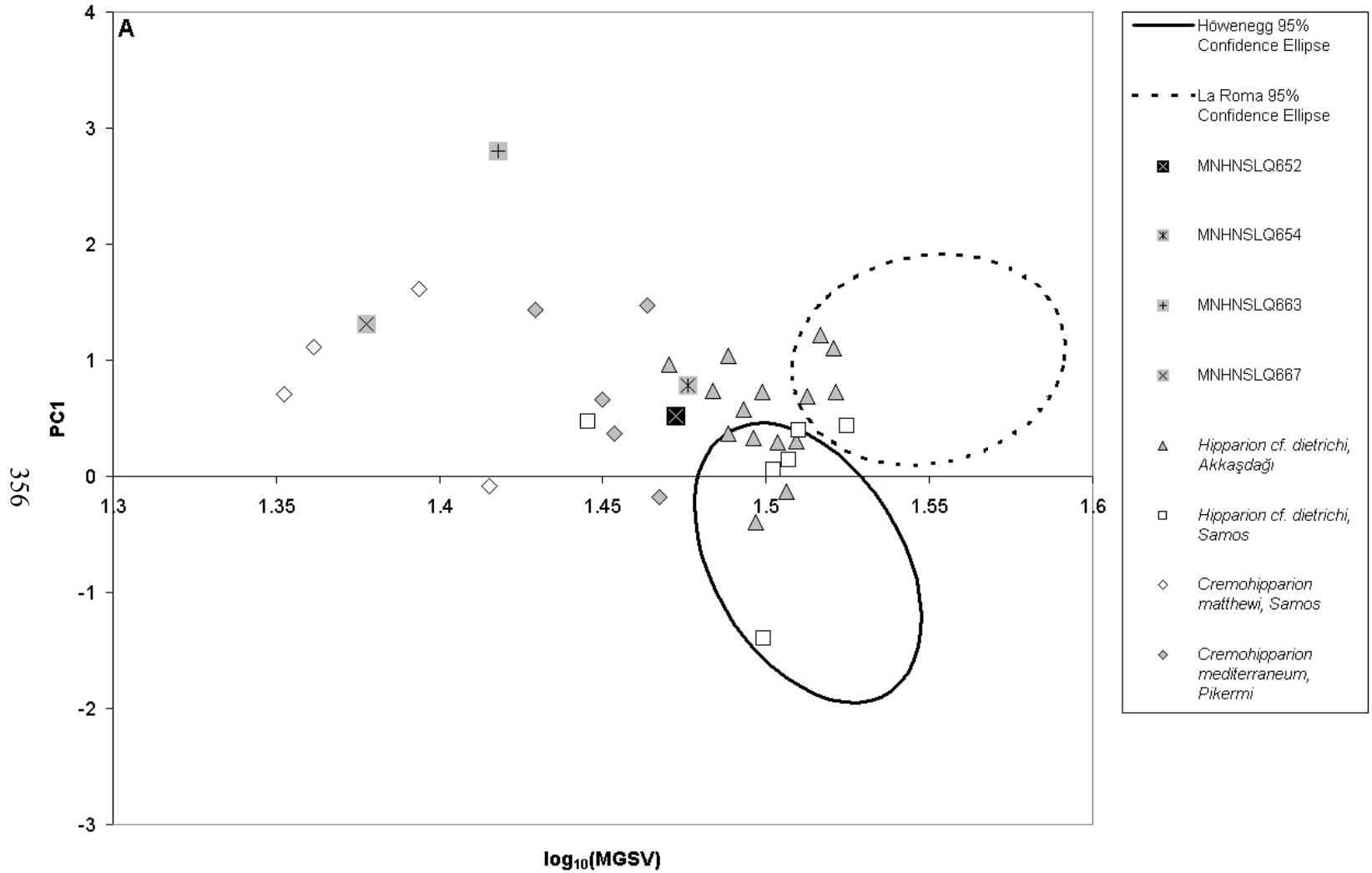


Figure 6.42: Plot of PC1 and log10(MGSV) for hipparionines from Saloniki with selected comparisons. A, MT III's; B, MC III's. Specimens from Saloniki are plotted with selected comparisons and 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

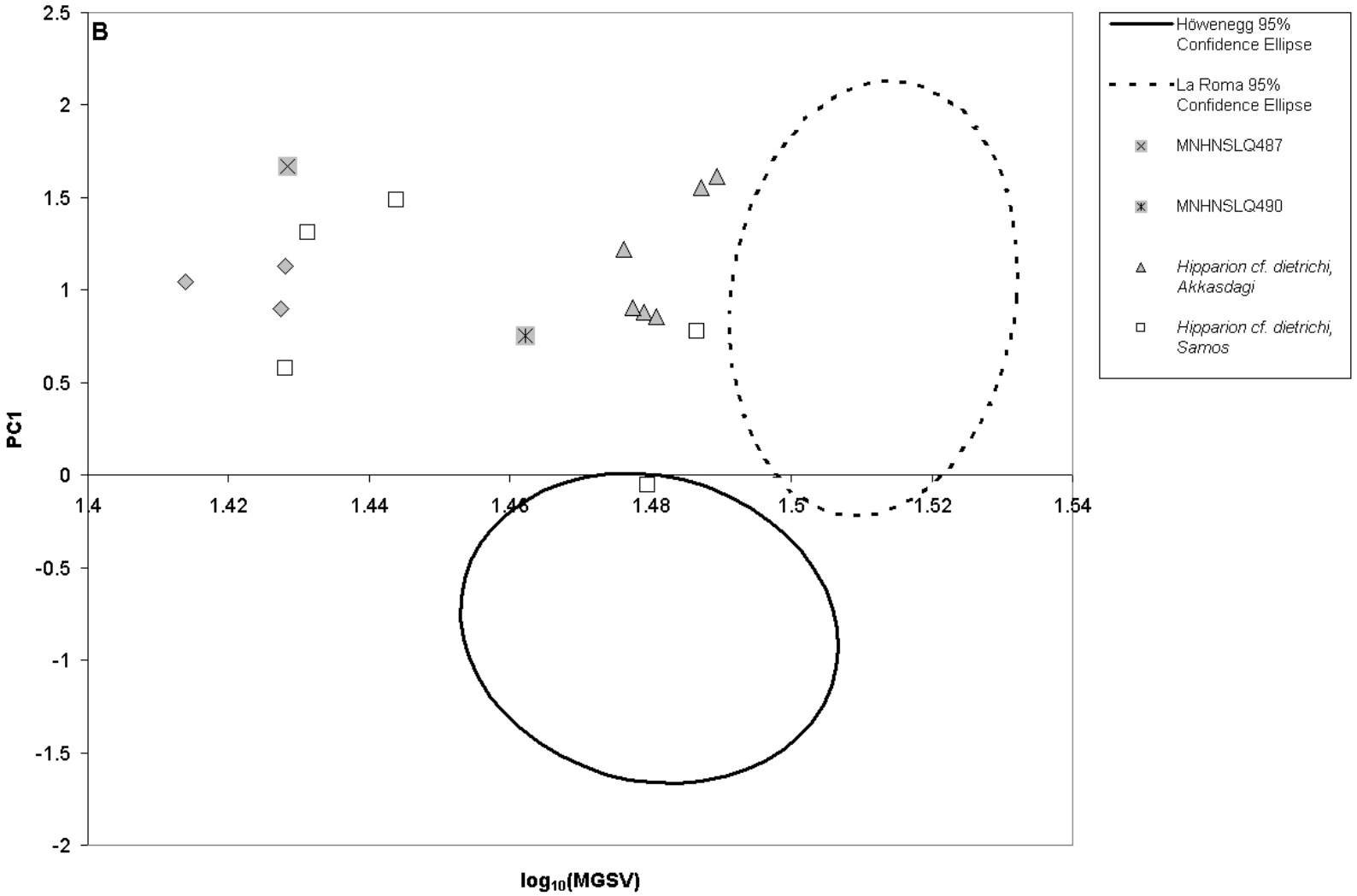


Figure 6.42: Plot of PC1 and log10(MGSV) for hipparionines from Saloniki with selected comparisons. A, MT III's; B, MC III's. Specimens from Saloniki are plotted with selected comparisons and 95% confidence ellipses for the Höwenegg and La Roma 2 standards.

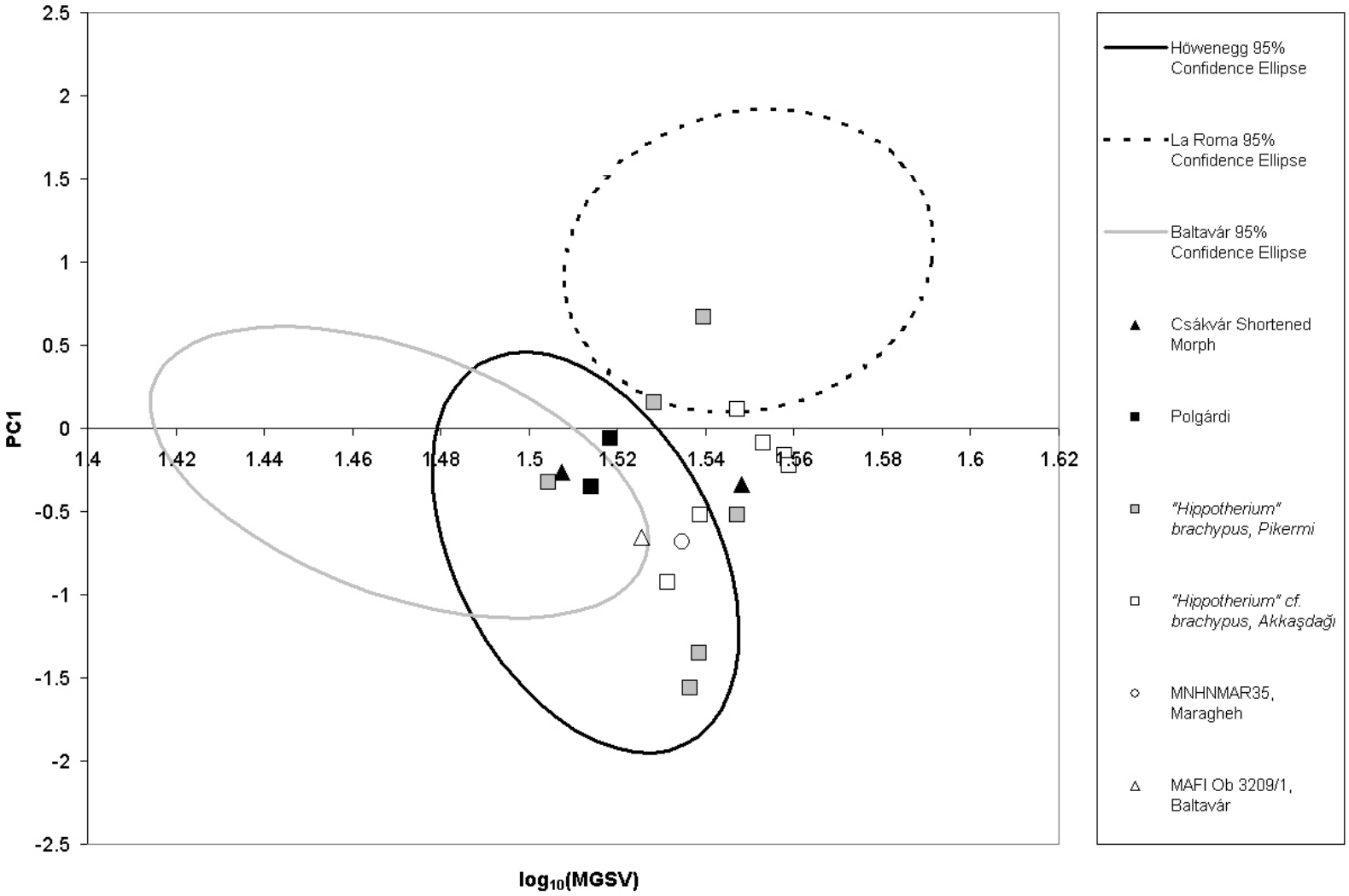


Figure 6.43: Plot of PC1 and $\log_{10}$(MGSV) for hipparionine MT III's attributed to *"Hippotherium"* cf. *brachypus*. MT III's attributed to *"Hippotherium"* cf. *brachypus* are plotted with 95% confidence ellipses for the Höwenegg and La Roma

PART IV: IMPLICATIONS FOR THE HOMINOIDEA

Chapter 7: Synthesis and Conclusions

The discussion of hipparion and bovid adaptations, diversity, and probable habitat preferences at different sites makes possible some comparisons and contrasts relevant to late Miocene hominoids. These observations can be divided into two broad categories. The first is positive associations between sites with hominoids and the kind of bovid and/or hipparion assemblages also found at these sites. The second category of observations could be termed negative associations. This latter category of observations results from comparisons between hominoid and non-hominoid sites and includes observations regarding sites from which hominoids are absent. These negative associations may be integrated with temporal and geographic scales.

This chapter discusses some positive and negative associations with hominoid sites and includes a brief evaluation of hominoid adaptations with respect to likely paleoenvironments. Finally, the hypotheses advanced in Chapter 1 are evaluated.

POSITIVE ASSOCIATIONS WITH HOMINOIDS

Table 7.1 summarizes the associations between hipparion assemblages and known hominoid sites. There appear to be two types of hipparion-hominoid associations. The first association is exemplified by Rudabánya in Hungary and Can Llobateres in Spain and the second is seen at Ravin de la Pluie in Greece and at locality 12 of the Sinap Formation in Turkey.

Rudabánya and Can Llobateres both appear to be less diverse with respect to hipparion species and do not include species with unambiguously high habitat scores indicative of the presence of a significant component of open and/or drier habitats. In

contrast, the Ravin de la Pluie and Sinap hipparion assemblages include 3 and at least 4 species respectively. In both cases, one of these species has a clearly very positive habitat score indicative of open habitats. Both *Cremohipparion macedonicum* at Ravin de la Pluie and *"Hipparion" uzunagizli* from Sinap have high habitat scores and both are very likely to have used fairly open habitats. Both species have MP III's that are both elongate and slender (figs. 6.8 & 6.22 in Chapter 6) suggesting both cursorial locomotion in open areas and harder substrates in drier habitats.

The diversity of the hipparions at Ravin de la Pluie and Sinap is worth some consideration. Both hipparion assemblages are diverse due to the apparent sympatry of "contra-morphs" and include species with a range of habitat scores from negative to positive. Each species appears to be somewhat unique from others at the same site in terms of habitat score. Thus, the paleoenvironments at Ravin de la Pluie and Sinap may well be distinguished most by the presence of a diversity of niches. Such diversity might imply the possibility of greater seasonality or of habitat fragmentation brought about by climate change (e.g., global cooling or increased aridity). The hipparion assemblages at Ravin de la Pluie and Sinap would appear to be diagnostic of what has been termed a 'proto-Pikermian' fauna in the Vallesian (Bernor et al., 2004).

The situation at Can Llobateres and probably at the other Spanish hominoid localities as well as that at Rudabánya implies that *Dryopithecus* was almost certainly tied to forested habitats. The hipparions from these sites do not indicate the presence of open habitats in any great abundance. This conclusion is consistent with the rest of the fauna from upper MN 9 hominoid sites. The occurrence of *Dryopithecus* at upper MN 9 localities has been linked with the presence of humid adapted elements such as tapirids, large castorids, tragulids, and flying-squirrels (Agusti & Llenas, 2004). The disappearance of *Dryopithecus* has been explained as due to an increase in deciduous trees as opposed to

an increase in grasslands (Agusti et al., 2003). This latter suggestion is not contradicted by the Piera hipparion (MN 11) which has intermediate habitat scores that do not suggest widespread grasslands.

Can Llobateres does appear to preserve two species of hipparion and one of these has somewhat more slender MP III's implying some kind of intermediate habitat and potentially some drier conditions. This result is probably most significant because it suggests a more diverse hipparion assemblage and potentially implies a greater diversity of resources than a hipparion assemblage that is monotypic with only a single species. Can Llobateres is on the cusp of the "mid-Vallesian crisis" marking the transition from MN 9 to MN 10 which appears to be one towards drier conditions (Agusti & Llenas, 2004). *"Hippotherium"* aff. *catalaunicum* has more slender MP III's and has the greater habitat score of the two hipparion species from Can Llobateres. It may be that at Can Llobateres an increase in aridity had already begun opening a niche for *"Hippotherium"* aff. *catalaunicum* with its more slender MP III's. This would be a small shift presaging the potentially larger changes of the "mid-Vallesian crisis."

Y0311 in the Siwaliks has already been discussed in Chapter 2 and is the only hominoid site that is better sampled in terms of bovid metapodials. Accordingly, the results of discriminant analysis of bovid metapodials reported in Chapter 2 support the conclusion that a diversity of habitats may have been available to the hominoid, *Sivapithecus parvada*, at Y0311 (Scott et al., 1999). The evidence relevant to the paleoenvironment of *Sivapithecus parvada* at Y0311 suggests the presence of closed canopies at Y0311 as well as more lightly wooded areas. Hipparions are not common at Y0311 and the assemblage is dominated by tragulids and bovids (Scott et al., 1999). However, one hipparion MP III analyzed here was assigned to *"Hipparion" antelopinum* which had positive mean habitat scores and likely used some open or lightly wooded

areas. The likelihood of some habitat diversity at Y0311 compares to the somewhat younger locality 12 of the Sinap Formation. However, the contrast between locality 12 and Y0311 is sharp in terms of hipparion abundance with hipparions common at Sinap. A dramatic increase in hipparion abundance recorded for the Sinap Formation appears to also occur in the Siwaliks at sites following Y0311 (Barry et al., 2002). Thus, it may be that changes in Siwalik bovids from earlier times seen at Y0311 (e.g., compare with Y0076, see Chapter 2) may prefigure changes leading to a general diversification of hipparions and increase in hipparion biomass. Thus, Y0311 may exhibit conditions incipient to the development of the 'proto-Pikermian' fauna (see Bernor et al., 2004) in the Vallesian of Greece and Turkey (i.e., Ravin de la Pluie and Sinap).

NEGATIVE ASSOCIATIONS WITH HOMINOIDS

Geographic Contrasts

Valles-Penedes Basin versus the Duero and Calatayud-Teruel Basins

Dryopithecus is part of the fauna at various Vallesian sites in the Valles-Penedes Basin (e.g., Can Llobateres) and the Seu d'Urgell Basin (El Firal). In contrast, sites of the Duero Basin and Calatayud-Teruel Basin inland from the Valles-Penedes lack hominoids. Thus, geographic distribution of hominoids may have been restricted to certain areas. For instance, proximity to the paleo-Mediterranean may have been an ameliorating climatic influence leading to more suitable hominoid environments in the Valles-Penedes. Indeed, a similar phenomenon might be at work at Rudabánya near the Pannonian lake.

Alternatively, the absence of hominoids from the Calatayud-Teruel Basin and Duero Basin may be due to their temporal distribution rather than geographic factors. Los Valles de Fuentidueña (Duero Basin) and Nombrevilla (Calatayud-Teruel Basin) predate the peak of hominoid occurrences (e.g., Can Llobateres) in Valles-Penedes and La Roma 2

(upper MN 10, Calatayud-Teruel Basin) postdates late (= MN 10) hominoid occurrences at La Tarumba in the Valles-Penedes Basin (Morales et al., 1999). Thus, the absence of hominoids from these sites may be due to a temporal rather than geographic trend.

Regardless of whether the absence of hominoids at Los Valles de Fuentidueña and La Roma 2 is ultimately linked to temporal or geographic causes, what is clear is that the proximate cause leading to the absence of hominoids from these two sites was likely ecological. The hipparion assemblages are very different at Los Valles de Fuentidueña and La Roma 2 compared to that at Can Llobateres. While Los Valles de Fuentidueña and La Roma 2 record a different species of hipparion, both sites are characterized by 1) only a single species of hipparion, 2) an open habitat adapted hipparion, and 3) a hipparion that numerically dominates the fossil assemblage. This is in sharp contrast to Can Llobateres and other Valles-Penedes sites where hipparion diversity may be greater (e.g., two species at Can Llobateres) and does not include a species with such elevated habitat scores as to indicate a clear adaptation to open habitats.

The occurrence of a single species of hipparion adapted to open habitats is a pattern worthy of note. Previously, more open environments have been linked to greater equid diversity (de Bonis et al., 1999). The cases of Los Valles de Fuentidueña and La Roma 2 contradict this model: at both sites equid diversity is low (one species) but this species is numerically dominant compared to other basal herbivores and adapted to more open habitats with elongate and slender MP III's and elevated habitat scores. This kind of hipparion fauna does not ever appear to be associated with the presence of hominoids. Hominoids associated with high habitat score hipparions are also associated with diverse hipparion faunas that also include hipparions with low habitat scores.

Eppelsheim versus Höwenegg

Eppelsheim is part of the 'Dinotheriumsande' deposits (Mainz, Germany) and is geographically not distant from Höwenegg (Hegau, Germany). It is also known for a complete femur of *Paidopithex rhenanus* POHLIG 1895 which has been referred to cf. *Dryopithecus* sp. (Andrews et al., 1996). More recently, the attribution of the Eppelsheim femur to *Dryopithecus* has been rejected (Köhler et al., 2002). However, Franzen et al. (2003) have recently reported the discovery of a phalange of a large hominoid at Eppelsheim. The probable presence of a hominoid at Eppelsheim in conjunction with the apparent absence of hominoids at Höwenegg has been considered somewhat puzzling (e.g.Franzen & Storch, 1999). It is worth raising the possibility that the Eppelsheim hominoid was in some way exploiting a niche that included seasonally open areas that were not present at Höwenegg. The case for this suggestion is suggested by the two hipparion MP III's from Eppelsheim with positive habitat scores and the contrast in diet between *Hippotherium primigenium* from Höwenegg and *Hippotherium primigenium* from Eppelsheim found by Kaiser (Kaiser, 2003). However, it would seem equally reasonable that the differences between Eppelsheim and Höwenegg in terms of ecology were small and the lack of hominoids at Höwenegg is the result of sampling error or taphonomic bias.

Temporal Contrasts

Sinap Formation

Clearly, modeling temporal trends in hipparion assemblages and hominoid faunas is difficult and usually hampered by poor sampling. Few cases of temporal trends can be productively interpreted. The Sinap Formation provides one example of a temporal succession of sites with possible implications for temporal changes in ecology.

The situation with respect to Sinap hipparions has been discussed recently in some depth (Bernor et al., 2003b; Scott et al., 2003) and will be summarized briefly here. The first occurrences of hipparions in the Sinap Formation are likely attributable to a single species not common in the fauna. The abundance of hipparion increases sharply through time and then flattens suggesting a carrying capacity was reached. As this carrying capacity is reached hipparion diversity appears to increase and niche separation would seem likely as several hipparion "contra-morphs" co-occur at locality 12 which is marked by abundant hipparion numbers and a diversity of four or five species (Bernor et al., 2003b; Scott et al., 2003).

The peak of hipparion diversity and abundance at locality 12 of the Sinap Formation (upper MN 9) is in conjunction with the presence of the hominoid *Ankarapithecus meteai*. One possibility is that the occurrence of *Ankarapithecus meteai* is linked to the same circumstances that allowed the diversification of hipparions at locality 12. Under this model, *Ankarapithecus meteai* could be tied to any number of habitats. One consequence of the presence of multiple habitats for a specific paleoenvironmental setting is the presence of edge or ecotone settings where different habitats meet. The presence of such habitats would appear likely at locality 12 and may not have existed (or have at least been less common) at earlier localities. The diversity of hipparions at locality 12 in contrast to Sinap localities prior to 10 Ma may indicate that these habitats were a late MN 9 phenomenon. The possibility that these edge or ecotone zones were critical to *Ankarapithecus meteai* draws some support from what little is known of its postcrania. Based on the morphology of the *Ankarapithecus* radius and phalanges, *Ankarapithecus* would appear to have been generally pronograde and have spent some time on the ground short of habitual terrestriality (Kappelman et al., 2003b). This is consistent with the use of

edge or ecotone environments which are implied by the diverse hipparion assemblage at locality 12.

Valles-Penedes Basin

Most recently, Agusti and Llenas (Agusti & Llenas, 2004) have tied the peak of *Dryopithecus* occurrences in the Valles-Penedes Basin to a period of increased humid and forested conditions during upper MN 9. However, *Dryopithecus* also occurs later during MN 10 (e.g., La Tarumba). By MN 11, *Dryopithecus* is extinct and it also appears absent from the late MN 10 (c. 9.0 – 9.2 Ma) vertebrate localities of the Terrassa section associated with an increase in deciduous trees (Agusti et al., 2003). The long record of occurrences of *Dryopithecus* from MN 8 to MN 10 suggests that the inference of optimal conditions during upper MN 9 should be taken with some caution.

The clearest association with the extinction of *Dryopithecus* would not appear to be the faunal changes of the MN 9/10 boundary ("mid-Vallesian crisis") but rather a late MN 10 shift towards a different floral association (see Agusti et al., 2003). This shift was not towards grasslands or necessarily more open environments and cover may have stayed constant. This change also appears to also have influenced hipparion assemblages. The MN 11 site of Piera appears to have only a single species of hipparion in contrast to Can Llobateres and Santiga (both MN 9 sites) which likely each have two species of hipparion. The Piera hipparion does not have a strong positive habitat score indicating a shift to more open habitats. Can Llobateres, Santiga, and Piera are the best sampled of the Valles-Penedes sites studied here and collectively would suggest a possible reduction in hipparion diversity as a result of changes in floral association to one marked by deciduous trees. This change in hipparion diversity could then be interpreted as having a cause common to that of the extinction of *Dryopithecus*.

The hypothesis that emerges from the Valles-Penedes record regarding environmental change and time would appear as follows: 1) *Dryopithecus* remains robust to fluctuations in humidity from MN 8 to MN 10, 2) an increase in aridity at the very end of MN 9 leads to a change in the character of the fauna towards more arid adapted taxa and the occurrence of a hipparion with more slender MP III's may be associated with these changes, and 3) by the end of MN 10 changes in floral association in favor of deciduous trees lead to a drop in hipparion diversity and the extinction of *Dryopithecus*.

The sequence suggested above would appear to be somewhat provincial with a different pattern occurring in the Calatayud-Teruel Basin. There MN 11 is associated not with a drop in hipparion diversity but with a contrasting increase in hipparion diversity as indicated by the addition of the very small species *Hipparion gromovae* at the MN 11 locality of Puente Minero (Alcalá, 1994).

Siwaliks

Possible temporal trends in the Siwaliks were discussed in Chapter 2 and the situation at Y0311 has already been noted above. Two points with respect to temporal trends would appear to be relevant. The first is that Y0311 appears to present a more diverse habitat than earlier Chinji localities. The presence of more lightly wooded areas seems likely. The necessary data are not available to compare Y0311 (c. 10 Ma) with later localities. However, Barry et al. (2002) report an increase in equids following Y0311 times - a trend similar to that seen at Sinap. Thus, Y0311 could represent a hominoid fauna that is in some ways an ecological precursor to the 'proto-Pikermian' faunas of Turkey and Greece. Ecologically, Y0311 might have been intermediate between the *Dryopithecus* sites of Can Llobateres and Rudabánya on the one hand, and the *Ouranopithecus* and *Ankarapithecus* sites in Greece and Turkey on the other hand.

HOMINOID ADAPTATIONS AND HABITAT

Hominoid adaptations appear to mirror the type of hipparion assemblage found at late Miocene Eurasian hominoid sites. The hipparion assemblages at Ravin de la Pluie and Sinap both correspond with the presence of megadont hominoids (Kappelman et al., 2003b) and in the case of *Ouranopithecus* the evidence for a dietary specialization for hard-object feeding is strong (Ungar & Kay, 1995; Ungar, 1996). In contrast, *Dryopithecus* with comparatively thin enamel has been reconstructed as eating soft fruit and leaves (Begun, 1994) and study of dental microwear appear to confirm a soft-fruit eating for *Dryopithecus* (Ungar, 1996). Thus, two apparent dietary modes for late Miocene Eurasian hominoids appear to correlate with probable habitat differences and differences in the adaptations and structure of hipparion assemblages that co-occur with these hominoids.

Similarly, locomotor adaptations for *Dryopithecus* and *Ankarapithecus* would appear to correlate with these same habitat differences. *Dryopithecus* appears to have adopted below branch suspensory postures during locomotion (Moyà-Solà & Köhler, 1996) in contrast with a likely more general pronograde (and perhaps somewhat terrestrial) locomotor repertoire for *Ankarapithecus* (Kappelman et al., 2003b).

Integration of hominoid adaptations with the paleoecological evidence presented here based on associated hipparion assemblages would clearly suggest two general niches for late Miocene hominoids in Eurasia. On the one hand, *Dryopithecus* would appear fairly tied to forested habitats likely including closed canopies and significant fresh fruit resources. These habitats would appear marked by lower hipparion diversity (one or two species) with adaptation for closed and/or wet habitats. In contrast, *Ankarapithecus* and *Ouranopithecus* appear to have occupied a niche not as marked by closed habitats. One possible habitat for these hominoids would be ecotonal settings implied by more diverse

hipparion assemblages with an apparent range of habitat adaptations. These habitats would be more suited to more general pronograde locomotion and would include open areas with hard-object food resources such as roots, tubers, seeds and nuts (see de Bonis & Koufos, 1994; Ungar, 1996).

ORIGINAL HYPOTHESES EVALUATED

Several hypotheses were put forward in Chapter 1 and the following section provides a brief evaluation of these. The original hypotheses are shown in italics and the conclusions based on this study concerning each hypothesis follow.

Specific Functional Hypotheses

1) *Relatively elongate metapodials are adaptive for open country running (and, by extension, open habitats) (Gregory, 1912).*

This hypothesis appears to be supported. In the case of extant equids (Chapter 5), a PCA resulted in a first principal component loading mainly with MP III relative length that explained nearly 40% of the variance. This component also appeared to separate species along a habitat gradient. Relative metapodial length was also part of the discriminant model that separated bovids into different habitat categories and relative length was greater in more open habitat bovids (Chapter 2). Hipparions thought to occupy different habitats were also separated by their degree of relative elongation (Chapter 6). For example, the La Roma 2 and Höwenegg hipparions contrasted sharply in terms of relative elongation.

2) *Relatively broad (mediolaterally expanded) metapodials are adaptive in closed or wet habitats (Gromova, 1949; Gromova, 1952).*

This hypothesis also appears supported. Habitat scores giving strong weight to relative metapodial slenderness separated extant equids, fossil hipparions, and extant

bovids along what appears to be a habitat gradient (Chapter 5, Chapter 6). The discriminant analysis of bovids suggests that relative metapodial breadth was the most significant variable separating bovids according to habitat cover (Chapter 2). Further work is needed to separate the influences of habitat cover from the influences of substrate state (reflecting humidity) on relative metapodial slenderness.

Paleoenvironmental Hypotheses

1) *The distribution of habitat types varies along an east to west gradient.*

Sampling must be considered inadequate to fully test this hypothesis. However, the 'proto-Pikermian' associations in Greece and Turkey appear different from those of western and central Europe (Chapter 6, Chapter 7).

2) *The distribution of habitat types varies with time.*

This appears almost certain but variation is not simple and monotonic (Chapter 6). Thus, some early Vallesian sites appear to represent open habitats but in general Turolian sites tend to preserve hipparion assemblages with greater habitat scores. For example, this trend can be seen in the habitat scores of specimens attributed to *"Hippotherium"* cf. *brachypus*.

3) *The distribution of habitat types varies with global climate.*

Sampling of hominoid habitats makes resolving relationships with global climate problematic. Figure 7.1 places Ravin de la Pluie, Can Llobateres, Sinap locality 12, Y0311, and Rudabánya in the context of a $\delta^{18}O$ curve (after Kennett, 1985) indicative of increases and decreases in ice volume. The occurrence of *Ouranopithecus* at Ravin de la Pluie falsifies an extreme relationship between hominoid extinctions and global cooling. The different habitat types at hominoid sites do not seem overly tied to global climate. For instance, Sinap locality 12 and Can Llobateres appear to represent different habitat types but are apparently contemporaneous during a period of probably milder temperature.

Better sampling of hominoid sites is clearly needed to advance more definitive conclusions regarding global climate variation charted in figure 7.1 and hominoid occurrences.

The distribution of habitat types is variable in time and space.

Significant spatial/geographic variation appears to be present. A good example would be the contrasting habitats and changes in habitats through time for the Valles-Penedes Basin versus the Calatayud-Teruel Basin (Chapter 6, Chapter 7).

Hominoids

1) *Hominoid species with suspensory adaptations are found in habitats with closed canopies while hominoids with generalized quadrupedal adaptations are found in habitats lacking closed canopies.*

This appears to be supported in general with the exception that more terrestrial hominoids like *Ankarapithecus* probably occurred in habitats where some closed canopy areas may have been present and these zones were marked most by habitat variability that included open habitats and ecotonal settings. Suspensory hominoids may have occurred in habitats with some open areas like seasonally extended grasslands.

2) *Late Miocene hominoid species tend to be found only in habitats with closed canopies.*

This does not appear to be the case. *Ankarapithecus* and *Ouranopithecus* would appear to be possible examples of edge or ecotone hominoids potentially not tied to closed canopies.

3) *Hominoid species that survive until the latest Miocene are found only in habitats with closed canopies*.

Ouranopithecus does not appear tied to closed canopies and is an MN 10 hominoid. Closed canopies could persist into MN 11 of the Valles-Penedes and may be distinguished from earlier closed canopy habitats by the dominance of deciduous trees.

3) *Well-sampled sites lacking hominoid species represent habitat types not available at hominoid fossil sites and possibly unsuitable for hominoids*.

This appears to be the case for sites dominated by a single species of open adapted hipparion such as Los Valles de Fuentidueña and La Roma 2.

CONCLUSIONS

It appears that two modes of association among habitat, hipparion diversity, and hominoid adaptations can be described for late Miocene hominoids in Eurasia. One mode is represented by lower hipparion diversity, hipparions adapted to closed habitats, and suspensory, frugivorous hominoids. Examples of sites that would fit this general pattern would be Rudabánya and Can Llobateres. In contrast, a second mode involves the association of a diverse and likely abundant hipparion fauna including open-adapted and closed-adapted forms with pronograde, hard object feeding hominoids. Sites that fit this mode would include Sinap locality 12 and Ravin de la Pluie. Y0311 in Pakistan is older and preserves far fewer hipparions in comparison to bovids and tragulids. The bovid fauna at Y0311 does however appear diverse. Y0311 could represent a habitat in transition towards those like that seen later at Sinap locality 12 as hipparions become more abundant. Hominoids do not appear to occur at sites with only a single open-adapted hipparion species.

Future study is needed to broaden the comparative framework advanced here. Integrating the postcranial adaptations of hipparions studied here with better interpretations of hipparion diets can further refine the paleoecological signal of hipparion assemblages. Studies of other taxa common at the sites evaluated here can offer added

refinements to the nature of hominoid paleoenvironments and depth to understanding of ecological processes relevant to hominoid evolution.

Table 7.1: Associations between hipparion assemblages and hominoid sites.

Site	Country	MN Zone	Hominoid Species	Hipparionine Diversity	Hipparionine Abundance	Hipparionine Habitats
El Firal	Spain	MN 9 (lower)	*Dryopithecus fontani*	1		
Santiga	Spain	MN 9	*Dryopithecus* sp.	1 to 2		subtropical forest
Can Ponsic	Spain	MN 9	*Dryopithecus crusafonti*	1		probably forested
Can Llobateres	Spain	MN 9 (upper)	*Dryopithecus laietanus*	2		subtropical forest with open patches (?seasonally extended grassy areas)
La Tarumba	Spain	MN 10	*Dryopithecus laietanus*	1		subtropical forest with open patches (?seasonally extended grassy areas)
Eppelsheim	Germany	MN 9	cf. *Dryopithecus* sp. (= *Paidopithex rhenanus*)	1	common	subtropical forest, seasonally extended grassy areas
Rudabánya	Hungary	MN 9 (upper)	*Dryopithecus brancoi*	1 to 2		subtropical forest, open areas distal to lake margin
Ravin de la Pluie	Greece	MN 10	*Ouranopithecus macedoniensis*	3		forest to open, diverse, ?more seasonal
Sinap loc. 12	Turkey	MN 9 (upper)	*Ankarapithecus meteai*	4 to 5	common	forest to open, diverse, ?more seasonal
Y0311(Siwaliks)	Pakistan	MN 9	*Sivapithecus parvada*	1 or more	uncommon	heavy to light cover

Table 7.1 cont.

Site	Hipparionine Species	Bovid Habitats	Mean Habitat Scores
El Firal	*"Hipparion"* sp. (smaller than *Hippotherium primigenium*?)		
Santiga	*"Hipparion"* cf. *depereti*		-1.01 (MC III), -1.06 (MT III)
Can Ponsic	*"Hippotherium"* cf. *catalaunicum*		
Can Llobateres	*"Hippotherium"* cf. *catalaunicum*, *"Hippotherium"* aff. *catalaunicum*	intermediate	-0.43 (MT III), -0.55 (MC III); -0.10 (MC III)
La Tarumba	*"Hippotherium"* aff. *catalaunicum*		-0.10 (MC III)
Eppelsheim	*Hippotherium primigenium*		0.09 (MC III), 0.87 (MT III)
Rudabánya	*Hippotherium intrans*, *"Hipparion"* sp. 2 (Vienna Basin)		-1.36 (MT III) ; -1.47, -1.22 (MC III)
Ravin de la Pluie	*Hippotherium primigenium*, *Cremohipparion macedonicum*, *"Hipparion"* aff. *depereti*		-0.31 (MT III); 1.32 (MT III); 0.06 (MT III)
Sinap loc. 12	*"Hipparion" kecigibi*, *"Hipparion" uzunagizli*, "Hipparion" sp. (Cursorial Morph), *Cormohipparion sinapensis*	intermediate	-0.45 (MC III), -0.83 (MT III); 0.98 (MC III), 0.89 (MT III); 0.60 (MC III), 0.27 (MT III); -0.30 (MC III), -0.53 (MT III)
Y0311(Siwaliks)	*"Hipparion" antelopinum*	intermediate	0.58 (MC III), 0.35 (MT III)

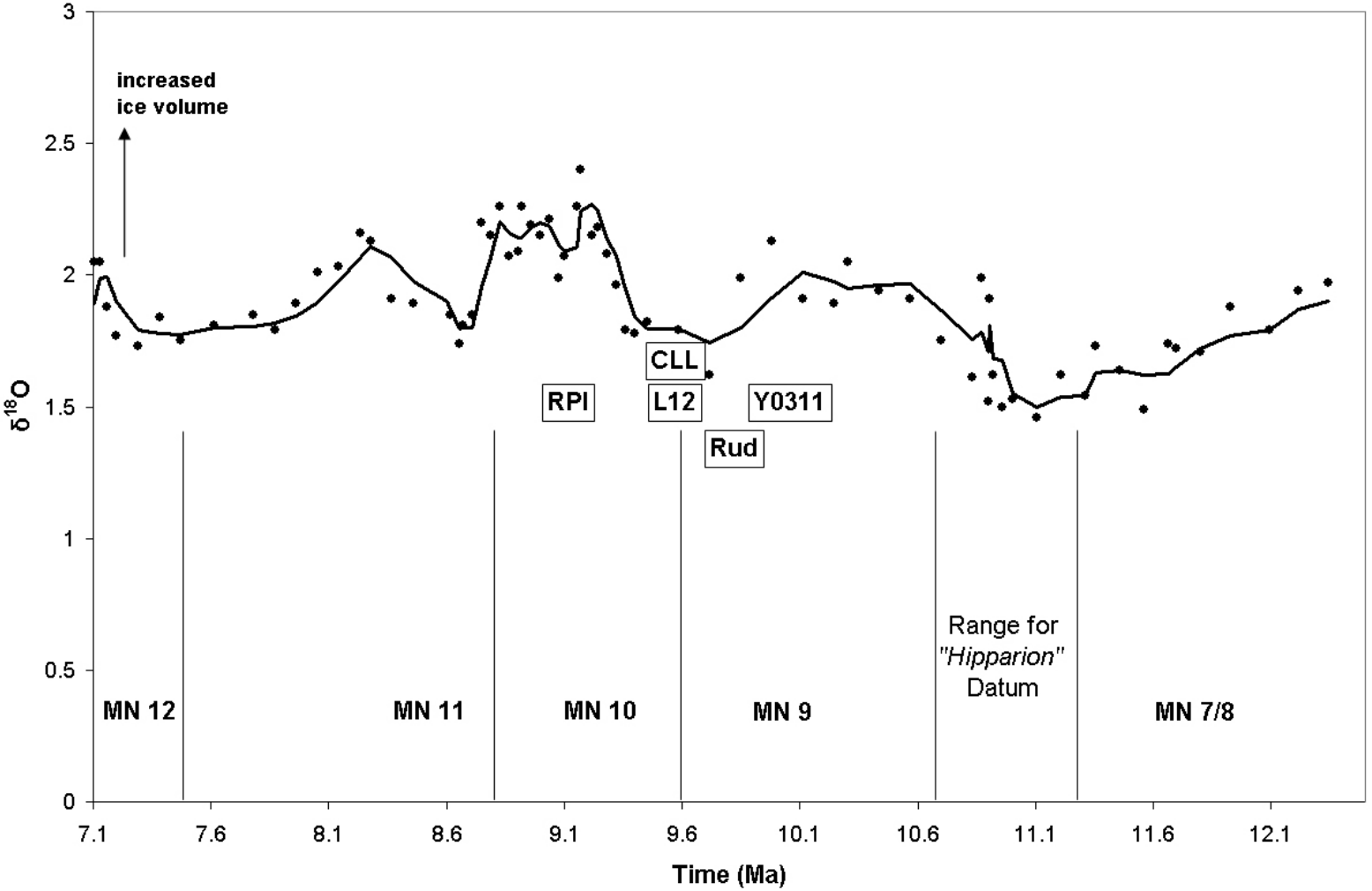


Figure 7.1: Climate change as measured by $\delta^{18}O$.Hominoid sites are shown in conjunction with $\delta^{18}O$ from DSDP site 588 after Kennett (1985). Ravin de la Pluie = RPL; Can Llobateres = CLL; Sinap loc. 12 = L12; Rudabánya -= RUD; Siwaliks loc. Y0311 = Y0311.

Appendices

APPENDIX A: EXTANT BOVID SAMPLE.

Table A1: Consensus mean body mass for bovids and antilocaprids.

Species	Habitat	Sex	Body mass (kg)	MGSV	Used	Sources
Antilocapridae						
Antilocaprinae						
Antilocaprini						
Antilocapra americana	Plains	Both	44	19.66		
		Male	51.5	20.01	x	Clancy and Croft, 1991*
Bovidae						
Aepycerotinae						
Aepycerotini						
Aepyceros melampus	Light cover	Both	49.8	21.2		Bourliere, 1961*; Bourliere, 1965*; Dowsett, 1966*; Hirst, 1975*; Jarman, 1971*; Lamprey, 1964*; Leuthold and Leuthold, 1976*; Mentis, 1970*; Montfort, 1972*; Watson, Graham, and Parker, 1969*; Writz, 1983*
		Male	58.1	21.93	x	Haltenorth and Diller, 1988; Kingdon, 1982; Kingdon, 1997; Rautenbach, 1982*; Smithers, 1971*; Smithers, 1983*; Wilson, 1975*
		Female	45	18.72	x	Haltenorth and Diller, 1988; Kingdon, 1982; Kingdon, 1997; Rautenbach, 1982*; Smithers, 1971*; Smithers, 1983*; Wilson, 1968*; Wilson, 1975*
Alcelaphinae						
Alcelaphini						

Alcelaphus buselaphus	Plains	Both	143.1	29.01		Bourliere, 1961*; Bourliere, 1965*; Geerling and Bokdam, 1973*; Green, 1979*; Happold, 1987*; Hoppe-Dominik, 1989*; Jamrozy, 1978*; Lamprey, 1964*; Leuthold and Leuthold, 1976*; Stewart and Zaphiro, 1963*; Watson, Graham, and Parker, 1969*
		Male	151.1	28.77	x	Baudenon, 1952*; Haltenorth and Diller, 1988; Kingdon, 1982; Haltenorth and Diller, 1988; Haltenorth and Diller, 1988; Smithers, 1983*
		Female	135.1	29.5	x	Haltenorth and Diller, 1988; Kingdon, 1982; Kingdon, 1997; Kingdon, 1982; Smithers, 1983*
Alcelaphus lichtensteini	Plains	Both	164.3	30.62		Dowsett, 1966*
		Male	177	30.62	x	Kingdon, 1982; Smithers, 1983*
Beatragus hunteri	Plains	Both	112.7	24.82		Kingdon, 1982; Kingdon, 1997; Stewart and Zaphiro, 1963*
		Male		25.24		
		Female		24.81		
Connochaetes gnou	Plains	Both	154.1	27.55		Stuart and Stuart, 1999
Connochaetes taurinus	Plains	Both	191	31.14		Bourliere, 1961*; Dowsett, 1966*; Stewart and Zaphiro, 1963*
		Male	212.5	32.44	x	Haltenorth and Diller, 1988; Kingdon, 1982; Sachs, 1967†; Smithers, 1971*
		Female	179	29.84	x	Haltenorth and Diller, 1988; Kingdon, 1982; Kingdon, 1997; Kingdon, 1982; Smithers, 1971*
Damaliscus dorcas	Plains	Both	65.7	21.83		Skinner, Dott, de Vos, and Millar, 1980*; Woodall and Skinner, 1993*
		Male	70.6	22.15	x	David, 1973†; Haltenorth and Diller, 1988; Kingdon, 1997; Smithers, 1983*
		Female	60.5	21.69	x	David, 1973†; Haltenorth and Diller, 1988; Kingdon, 1997; Smithers, 1983*
Damaliscus lunatus	Plains	Both	125.9	27.79		Bourliere, 1961*; Bourliere, 1965*; Green, 1979*; Haltenorth and Diller, 1988; Happold, 1987*; Montfort, 1972*; Stewart and Zaphiro, 1963*; Wilson, 1975*

		Male	137	28.05	x	Kingdon, 1982; Kingdon, 1997; Sachs, 1967†; Kingdon, 1997; Talbot and Talbot, 1962*
		Female	120.8	27.43	x	Kingdon, 1982; Kingdon, 1997; Sachs, 1967†; Kingdon, 1997; Talbot and Talbot, 1962*
Antilopinae						
Antilopini						
Antidorcas marsupialis	Plains	Both	38.7	18.58		Groves, 1981†
		Male	42.1	18.99	x	Bigalke, 1963b†; Kingdon, 1997; Smithers, 1971†; Smithers, 1971*
Antilope cervicapra	Plains	Both	34.2	17.31		Eisenberg and Seidensticker, 1976*
		Male	39.5	18.55	x	Krishnan, 1972*; Roberts, 1977*
		Female	35.3	16.45	x	Roberts, 1977*
Eudorcas rufifrons	Plains	Both	25.4	16.56		Happold, 1987*
		Male	28.8	16.56	x	Haltenorth and Diller, 1988; Kingdon, 1997
Eudorcas thomsoni	Plains	Both	20.3	16.17		Bourliere, 1961*; Estes, 1967*; Jamrozy, 1978*; Estes, 1967*; Estes, 1967*; Writz, 1983*
		Male	23.8	16.35	x	Haltenorth and Diller, 1988; Kingdon, 1982; Talbot and Talbot, 1962*
		Female	18.2	15.8	x	Haltenorth and Diller, 1988; Hviderg-Hansen, 1970*; Kingdon, 1982
Gazella gazella	Plains	Both	20.2	14.15		Baharav, 1974*
		Female		14.15		
Litocranius walleri	Light cover	Both	36.6	19.16		Leuthold and Leuthold, 1976*
		Male	43	19.83	x	Haltenorth and Diller, 1988; Kingdon, 1982; Kingdon, 1997
		Female	34.2	18.71	x	Haltenorth and Diller, 1988; Kingdon, 1982; Kingdon, 1997
Nanger granti	Plains	Both	52.9	21.25		Bourliere, 1961*; Estes, 1967*; Jamrozy, 1978*; Kingdon, 1997; Leuthold and Leuthold, 1976*; Stewart and Zaphiro, 1963*; Writz, 1983*

		Male	69.1	21.87	x	Haltenorth and Diller, 1988; Kingdon, 1982; Kingdon, 1997; Talbot and Talbot, 1962*
		Female	46.7	20	x	Haltenorth and Diller, 1988; Kingdon, 1982; Kingdon, 1997
Nanger soemmerringi	Plains	Both	40	17.03		Haltenorth and Diller, 1988; Kingdon, 1982
		Male		17.15		
		Female		16.91		
Neotragini						
Madoqua guentheri	Heavy cover	Both	4.6	8.93		Haltenorth and Diller, 1988; Kingdon, 1997
		Male		8.95		
		Female		8.92		
Madoqua kirki	Heavy cover	Both	11.8	9.68		Haltenorth and Diller, 1988; Kingdon, 1997; Lamprey, 1964*; Smithers, 1983*
		Male	5.1	9.68	x	Kingdon, 1982
Madoqua sp.	Heavy cover	Both		9.26		
		Male		9.6		
		Female		9.09		
Neotragus batesi	Forest	Both	3.8	6.92		Haltenorth and Diller, 1988; Happold, 1987*; Kingdon, 1997
		Male		6.92		
Nesotragus moschatus	Forest	Both	17.3	7.93		Haltenorth and Diller, 1988; Kingdon, 1997
		Male	5	7.93	x	Smithers, 1983*
Oreotragus oreotragus	Mountain	Both	12.4	13.02		Bourliere, 1961*; Dunbar, 1978*; Haltenorth and Diller, 1988; Happold, 1987*; Kingdon, 1982; Kingdon, 1997; Mentis, 1970*; Writz, 1983*
		Male	11.2	12.94	x	Hofman, 1973; Smithers and Wilson, 1979†; Rautenbach, 1982*; Smithers, 1971*; Rautenbach, 1982*; Wilson, 1975*
		Female	13	13.22	x	Hofman, 1973; Smithers and Wilson, 1979†; Smithers, 1971*; Smithers, 1983*; Wilson, 1975*

Ourebia ourebi	Light cover	Both	13.9	14.84		Bourliere, 1965*; Dowsett, 1966*; Geerling and Bokdam, 1973*; Green, 1979*; Haltenorth and Diller, 1988; Happold, 1987*; Kingdon, 1997; Montfort and Montfort, !974*; Montfort, 1972*; Oliver, Short, and Hanks, 1972*
		Male	13.9	15.13	x	Blancou, 1962*; Kingdon, 1982; Rautenbach, 1982*; Smithers, 1983†
		Female	14.9	14.27	x	Baudenon, 1952*; Blancou, 1962*; Kingdon, 1982; Blancou, 1962*; Smithers, 1983†
Raphicerus campestris	Light cover	Both	11.3	12.66		Bourliere, 1961*; Haltenorth and Diller, 1988; Kingdon, 1982; Kingdon, 1997; Mentis, 1970*; Woodall and Skinner, 1993*; Writz, 1983*
		Male	10.5	12.73	x	Cloete and Kok, 1986*; Rautenbach, 1982*; Smithers, 1971*; Rautenbach, 1982*; Wilson, 1975*
		Female	11.3	12.54	x	Smithers, 1971*; Smithers, 1983†; Wilson, 1975*
Raphicerus sharpei	Light cover	Both	8	11.46		Dowsett, 1966*; Kingdon, 1982; Kingdon, 1997
		Female	7.9	11.46	x	Smithers, 1983*; Wilson, 1975*
Saigini						
Saiga tatarica	Plains	Both	36.5	16.35		
		Male	41.8	16.81	x	Heptner, Nasimovich, and Bannikov, 1989*
		Female	31.2	15.33	x	Heptner, Nasimovich, and Bannikov, 1989*
Bovinae						
Boselaphini						
Boselaphus tragocamelus	Heavy cover	Both	193.8	32.5		Dinerstein, 1980*; Roberts, 1977*
		Male	250.3	31.13	x	MacDonald, 1984; Roberts, 1977*; Sheffield, Fall, and Brown, 1983‡
Tetracerus quadricornis	Heavy cover	Both	20.6	14.32		Krishnan, 1972*; MacDonald, 1984; Nowak, 1999
		Male		14.15		

		Female		14.54		
Bovini						
Anoa depressicornis	Forest	Both	225	21.27		Grzimek, 1975[‡]; MacDonald, 1984
		Male		22.08		
		Female		18.22		
Anoa mindorensis	Forest	Both	260	31.07		Custodio, Lepiten, and Heaney, 1996[‡]; MacDonald, 1984
		Male		30.24		
Bison bison athabaskae	Light cover	Both	949	43.99		
		Male	949	47.01	x	Bayrock,1964[*]
		Female		41.18		
Bison bison bison	Plains	Both	681.5	43.86		
		Male	818	43.43	x	MacDonald, 1984
		Female	545	47.51	x	MacDonald, 1984
Bos gaurus	Heavy cover	Both	853.2	44.08		Dinerstein, 1989[*]; Harrison, 1966[*]; Johnsingh, 1983[*]; Harrison, 1966[*]; Medway, 1978[*]
		Male		43.47		
Bos grunniens	Mountain	Both		32.04		
		Male		32.8		
		Female		28.79		
Bos sauveli	Heavy cover	Both	800	34.88		Lekagul and McNeely, 1977[*]
		Female		35.25		
Bubalis bubalis	Heavy cover	Both		32.18		
		Female		32.18		
Syncerus caffer caffer	Light cover	Both	614.4	48.11		Haltenorth and Diller, 1988
		Male	683	48.78	x	Kingdon, 1982; Sinclair, 1977b[†]
Syncerus caffer nanus	Heavy cover	Both	334.2	39.01		Haltenorth and Diller, 1988; Henshaw and Geerling, 1973[*]; Kingdon, 1982
		Male	473	39.3	x	Henshaw and Geerling, 1973[*]; Kingdon, 1982

		Female		38.44		
Tragelaphini						
Tragelaphus angasi	Heavy cover	Both	91.1	23.46		Mentis, 1970*; Woodall and Skinner, 1993*
		Male	113.5	23.46	x	Estes, 1991; Haltenorth and Diller, 1988; Kingdon, 1997; Haltenorth and Diller, 1988; Haltenorth and Diller, 1988; Stuart and Stuart, 1999
Tragelaphus derbianus	Light cover	Both	599.5	44.38		Happold, 1987*
		Male	678.5	44.38	x	Kingdon, 1982
Tragelaphus eurycerus	Forest	Both	284.7	33.88		
		Male	325	34.37	x	Geist and Bayer, 1988*; Haltenorth and Diller, 1988; Kingdon, 1982
		Female	244.3	31.72	x	Geist and Bayer, 1988*; Haltenorth and Diller, 1988; Kingdon, 1982
Tragelaphus imberbis	Heavy cover	Both	93.9	24.84		Hirst, 1975*; Jarman, 1971*; Leuthold and Leuthold, 1976*; Mentis, 1970*
		Male	100.1	25.9	x	Estes, 1991; Haltenorth and Diller, 1988; Kingdon, 1982
		Female	71.2	23.26	x	Estes, 1991; Haltenorth and Diller, 1988; Kingdon, 1982
Tragelaphus oryx	Light cover	Both	403.6	40.58		Bourliere, 1961*; Bourliere, 1965*; Dowsett, 1966*; Holmeyr and Lenssen, 1975*; Jamrozy, 1978*; Lamprey, 1964*; Leuthold and Leuthold, 1976*; Mentis, 1970*; Montfort, 1972*; Stewart and Zaphiro, 1963*; Watson, Graham, and Parker, 1969*; Woodall and Skinner, 1993*; Writz, 1983*
		Male	646.7	43.42	x	Estes, 1991; Haltenorth and Diller, 1988; Kingdon, 1982
		Female	430.8	37.53	x	Estes, 1991; Haltenorth and Diller, 1988; Kingdon, 1982
Tragelaphus scriptus	Forest	Both	43.7	18.72		Bourliere, 1961*; Bourliere, 1965*; Dowsett, 1966*; Dunbar, 1978*; Geerling and Bokdam, 1973*; Happold, 1987*; Hoppe-Dominik, 1989*; Mentis, 1970*; Wilson, 1975*; Writz, 1983*
		Male	48.4	19.29	x	Blancou, 1962*; Estes, 1991; Haltenorth and Diller, 1988; Estes, 1991; Estes, 1991; Smithers, 1983*

		Female	33	18.14	x	Blancou, 1962*; Estes, 1991; Haltenorth and Diller, 1988; Estes, 1991; Estes, 1991; Smithers, 1983*
Tragelaphus spekei	Heavy cover	Both	87.3	23.97		Happold, 1987*
		Male	102.7	25.27	x	Haltenorth and Diller, 1988; Kingdon, 1982; Smithers, 1971*
		Female	63	21.36	x	Haltenorth and Diller, 1988; Kingdon, 1982
Tragelaphus strepsiceros	Heavy cover	Both	208.8	31.37		Bourliere, 1961*; Dowsett, 1966*
		Male	251.7	31.26	x	Haltenorth and Diller, 1988
		Female		33.19		Haltenorth and Diller, 1988; Kingdon, 1982; Smithers, 1983*
Caprinae						
Caprini						
Ammotragus lervia	Mountain	Both	92.5	20.6		
		Female	47.5	16.05	x	Haltenorth and Diller, 1988
Ovis ammon	Mountain	Both	117.5	23.51		MacDonald, 1984
		Male		26.46		
		Female		21.55		
Pantholopini						
Pantholops hodgsoni	Plains	Both	36.5	16.96		
Rupicaprini						
Budorcas taxicolor	Mountain	Both		31.12		
		Male		31.12		
Myotragus balearicus	Mountain	Both		17.5		
Naemorhedus crispus	Mountain	Both	30	16.29		
		Female	30	16.29	x	Yamamoto, 1967*
Naemorhedus goral	Mountain	Both	28.3	16.67		Green, 1987*; Lekagul and McNeely, 1977*; Roberts, 1977*
		Male	32	16.57	x	Heptner, Nasimovich, and Bannikov, 1989*
		Female		16.8		

Naemorhedus sumatraensis	Mountain	Both	100.5	25.69		Green, 1987*; Harrison, 1966*; Lekagul and McNeely, 1977*; Harrison, 1966*; Harrison, 1966*; Nowak, 1999
		Male		25.23		
		Female		26.38		
Naemorhedus swinhoei	Mountain	Both		15.8		
		Male		15.8		
Oreamnos americanus	Mountain	Both	84.5	23.68		Soper, 1973*
		Male	88.5	24.73	x	Houston, Robbins, and Stevens, 1989*; Soper, 1973*
		Female	70	22.35	x	Houston, Robbins, and Stevens, 1989*
Rupicapra rupicapra	Mountain	Both	29.6	18.3		Clarke and Henderson, 1979*
		Male	40	18.3	x	Heptner, Nasimovich, and Bannikov, 1989*
Cephalophinae						
Cephalophini						
Cephalophus dorsalis	Forest	Both	18.8	13.63		Bourliere, 1961*; Dubost, 1978*; Dubost, 1984*; Haltenorth and Diller, 1988; Happold, 1987*; Kingdon, 1982; Kingdon, 1997
		Male		13.74		
		Female	11.6	13.46	x	Baudenon, 1952*; Coe, 1975*
Cephalophus leucogaster	Forest	Both	16.4	12.9		Dubost, 1984*; Haltenorth and Diller, 1988; Kingdon, 1982; Kingdon, 1997
		Male		12.7		
		Female		13.03		
Cephalophus sylvicultor	Forest	Both	61.5	21.36		Dubost, 1978*; Dubost, 1984*; Haltenorth and Diller, 1988; Happold, 1987*; Kingdon, 1982; Kingdon, 1997; Maclatchy, 1951*
		Male	43	21.11	x	Baudenon, 1952*
		Female		21.69		
Cephalophus weynsi	Forest	Both		11.95		
		Male		11.95		
Philantomba monticola	Forest	Both	5.7	8.06		Haltenorth and Diller, 1988; Kingdon, 1997

		Female	5.1	8.06	x	Dubost, 1980[†]; Smithers, 1983[*]
Sylvicapra grimmia	Light cover	Both	15.2	13.12		Blancou, 1962[*]; Bourliere, 1961[*]; Bourliere, 1965[*]; Dowsett, 1966[*]; Green, 1979[*]; Haltenorth and Diller, 1988; Happold, 1987[*]; Woodall and Skinner, 1993[*]
		Male	17.2	13.65	x	Kingdon, 1982; Rautenbach, 1982[*]; Smithers, 1971[*]; Rautenbach, 1982[*]; Rautenbach, 1982[*]; Wilson, 1975[*]
		Female	17	13.03	x	Baudenon, 1952[*]; Kingdon, 1982; Mitchell, Shenton, and Uys, 1965[*]; Rautenbach, 1982[*]; Smiothers, 1983[†]; Smithers, 1971[*]; Wilson and Clarke, 1967[†]; Wilson, 1968[*]; Wilson, 1975[*]
Hippotraginae						
Hippotragini						
Addax nasomaculatus	Plains	Both	85.8	24.15		Hufnagl, 1972[*]
Hippotragus equinus	Light cover	Both	241.2	33.98		Bourliere, 1961[*]; Bourliere, 1965[*]; Dowsett, 1966[*]; Geerling and Bokdam, 1973[*]; Green, 1979[*]; Happold, 1987[*]; Montfort, 1972[*]
		Male	280	33.43	x	Haltenorth and Diller, 1988; Kingdon, 1982
		Female	256.3	34.8	x	Haltenorth and Diller, 1988; Kingdon, 1982; Wilson, 1968[*]
Hippotragus niger	Light cover	Both	212.4	31.28		Dowsett, 1966[*]
		Male	231.5	31.79	x	Haltenorth and Diller, 1988; Kingdon, 1982; Smithers, 1971[*]; Smithers, 1983[*]
		Female	190	29.86	x	Haltenorth and Diller, 1988; Kingdon, 1982
Oryx beisa	Plains	Both	169	28.53		
		Male	176	28.1	x	Kingdon, 1982
		Female	162	28.97	x	Kingdon, 1982
Oryx dammah	Plains	Both	195	27.25		Haltenorth and Diller, 1988; Petit, Poilane, Poilane, Seitre and Seitre, 1989[*]
Oryx gazella	Plains	Both	188.8	29.57		Haltenorth and Diller, 1988; Woodall and Skinner, 1993[*]

		Male	199.8	29.45	x	Kingdon, 1982; Petit, Poilane, Poilane, Seitre and Seitre, 1989*; Smithers, 1971*; Talbot and Talbot, 1962*
		Female	186.8	29.68	x	Kingdon, 1982; Petit, Poilane, Poilane, Seitre and Seitre, 1989*; Smithers, 1971*
Oryx leucoryx	Plains	Both	63.2	25.51		Haltenorth and Diller, 1988
Reduncinae						
Reduncini						
Kobus ellipsiprymnus	Heavy cover	Both	175.4	31.93		Bourliere, 1961*; Bourliere, 1965*; Dowsett, 1966*; Geerling and Bokdam, 1973*; Green, 1979*; Hoppe-Dominik, 1989*; Jamrozy, 1978*; Lamprey, 1964*; Spinage, 1982†; Wilson, 1975*; Writz, 1983*
		Male	234	32.28	x	Haltenorth and Diller, 1988; Kingdon, 1982; Kingdon, 1997; Spinage, 1982†
		Female	190	29.84	x	Haltenorth and Diller, 1988; Kingdon, 1982; Kingdon, 1997
Kobus kob	Light cover	Both	68.8	23.22		Bourliere, 1961*; Bourliere, 1965*; Geerling and Bokdam, 1973*; Green, 1979*; Happold, 1987*; Hoppe-Dominik, 1989*; Montfort, 1972*; Wilson, 1975*
		Male	96.5	23.56	x	Haltenorth and Diller, 1988; Kingdon, 1982; Kingdon, 1997
		Female	59.1	22.81	x	Buechner, Morrison, and Leuthold, 1966*; Haltenorth and Diller, 1988; Kingdon, 1982; Kingdon, 1997
Kobus leche	Light cover	Both	96.6	23.07		
		Male	108.1	23.07	x	Haltenorth and Diller, 1988; Kingdon, 1997; Robinette and Child, 1964†; Siegfried, 1990*; Smithers, 1971*; Smithers, 1983*; Stuart and Stuart, 1999
Kobus megaceros	Heavy cover	Both	90	23.62		
		Male	105	24.99	x	Haltenorth and Diller, 1988; Kingdon, 1997
		Female	75	22.94	x	Haltenorth and Diller, 1988; Kingdon, 1997

Redunca arundinum	Light cover	Both	51.3	22.6		Bourliere, 1965*; Dowsett, 1966*; Mentis, 1970*; Montfort, 1972*; Wilson, 1975*; Woodall and Skinner, 1993*; Writz, 1983*
		Male	67.5	22.6	x	Haltenorth and Diller, 1988; Kingdon, 1982; Kingdon, 1997; Kingdon, 1982; Kingdon, 1982; Wilson, 1975*
Redunca fulvorufula	Light cover	Both	28.4	16.92		Haltenorth and Diller, 1988; Happold, 1987*; Oliver, Short, and Hanks, 1972*
		Male	30.1	16.62	x	Kingdon, 1982; Kingdon, 1997; Smithers, 1983*
		Female	29	17.05	x	Irby, 1979*; Kingdon, 1982; Kingdon, 1997; Smithers, 1983*
Redunca redunca	Light cover	Both	45.2	20.12		Green, 1979*; Happold, 1987*
		Male	51.9	20.68	x	Haltenorth and Diller, 1988; Kingdon, 1982; Kingdon, 1997
		Female	41.8	19.75	x	Haltenorth and Diller, 1988; Kingdon, 1982; Kingdon, 1997

* as reported by Silva land Downing (1995).
† as reported by Estes (1991).
‡ as reported by Nowak (1999).

Table A2: Summary by species of variables derived from length, proximal epiphyseal measurements, and CV1 based on analysis of complete metapodials.

Species	Habitat	Elem.	*N*	MLEN	PML	PAP	PNML or MGML	CV1	Rot. CV1
Antilocapridae									
Antilocaprinae									
Antilocaprini									
Antilocapra americana	Plains	MT	11	0.0586	0.0682	0.0032	.	-1.4061	-1.9276
				(0.0104)	(0.0125)	(0.0145)		(0.5356)	(0.5823)
		MC	6	0.0721	-0.0063	-0.0015	-0.0615	-0.8782	-2.4474
				(0.005)	(0.0137)	(0.0088)	(0.0452)	(0.3838)	(0.5145)
Bovidae									
Aepycerotinae									
Aepycerotini									
Aepyceros melampus	Light cover	MT	11	0.0892	0.0624	0.0097	-0.0617	-1.0977	-1.0414
				(0.0204)	(0.0084)	(0.0068)	(0.0482)	(0.5357)	(0.5815)
		MC	11	0.0996	-0.0276	-0.0044	-0.0128	-1.0008	-1.5869
				(0.0201)	(0.0149)	(0.012)	(0.0182)	(0.5566)	(0.4809)
Alcelaphinae									
Alcelaphini									
Alcelaphus buselaphus	Plains	MT	9	0.0531	0.0812	0.0007	-0.0043	-1.2892	-1.3316
				(0.01)	(0.0131)	(0.0122)	(0.0676)	(0.9129)	(0.8662)
		MC	9	0.0765	0.0004	-0.0159	-0.004	-1.9611	-2.6714
				(0.0122)	(0.0173)	(0.0144)	(0.0349)	(0.751)	(0.2991)
Alcelaphus lichtensteini	Plains	MT	1	0.0455	0.0816	0.0119	0.0123	-0.7709	-0.9493
		MC	1	0.0618	-0.0164	0.0049	-0.0098	-1.7688	-1.989
Beatragus hunteri	Plains	MT	3	0.0826	0.0811	0.0248	-0.2092	-1.8801	-1.3693
				(0.0031)	(0.0091)	(0.0036)	(0.0953)	(0.8248)	(0.9291)

		MC	3	0.0898	-0.0013	-0.0114	0.0306	-2.6267	-2.5669
				(0.0057)	(0.0011)	(0.0071)	(0.0063)	(0.1542)	(0.2363)
Connochaetes gnou	Plains	MT	4	-0.0052	0.0981	0.0205	0.0409	-1.3548	-1.4834
				(0.0058)	(0.0128)	(0.0081)	(0.0359)	(0.3776)	(0.3684)
		MC	4	-0.0295	0.0158	0.0038	0.0372	-1.2281	-2.8074
				(0.0032)	(0.003)	(0.0078)	(0.0111)	(0.2535)	(0.4078)
Connochaetes taurinus	Plains	MT	6	0.0104	0.0852	0.0125	0.0014	-1.0818	-1.4931
				(0.0081)	(0.0143)	(0.0219)	(0.0505)	(0.5013)	(0.5297)
		MC	6	0.0083	0.0127	-0.0077	0.007	-0.9647	-2.3292
				(0.0094)	(0.0141)	(0.015)	(0.0205)	(0.5962)	(0.6019)
Damaliscus dorcas	Plains	MT	5	0.0629	0.0751	0.0118	0.0081	-2.7458	-2.6384
				(0.0103)	(0.0157)	(0.007)	(0.0404)	(0.164)	(0.2186)
		MC	5	0.0597	-0.0178	0.006	0.003	-2.5124	-2.497
				(0.0107)	(0.0167)	(0.0174)	(0.0172)	(0.5419)	(0.5535)
Damaliscus lunatus	Plains	MT	7	0.0598	0.0756	0.0078	-0.0255	-2.1541	-2.1244
				(0.0172)	(0.0134)	(0.0051)	(0.0872)	(0.2658)	(0.291)
		MC	7	0.0807	-0.0086	-0.0032	-0.0073	-2.4892	-2.7191
				(0.0124)	(0.0131)	(0.0102)	(0.0238)	(0.5038)	(0.4629)
Antilopinae									
Antilopini									
Antidorcas marsupialis	Plains	MT	5	0.104	0.0732	0.0296	-0.1103	-2.2469	-2.0115
				(0.0077)	(0.0057)	(0.0106)	(0.0428)	(0.6693)	(0.6182)
		MC	5	0.1058	-0.0006	0.0092	-0.0145	-2.0118	-2.8539
				(0.0116)	(0.027)	(0.0174)	(0.0156)	(0.5655)	(0.7058)
Antilope cervicapra	Plains	MT	3	0.0511	0.0807	0.0334	-0.0456	-1.495	-1.5093
				(0.0066)	(0.0097)	(0.0117)	(0.0362)	(0.9701)	(1.0171)
		MC	3	0.0741	0.0034	0.0109	-0.0112	-0.9525	-1.942
				(0.0112)	(0.0061)	(0.0091)	(0.0354)	(0.6211)	(1.3045)
Eudorcas rufifrons	Plains	MT	1	0.0591	0.0673	0.0146	-0.0753	-1.7383	-1.8979

		MC	1	0.0676	-0.012	-0.0104	-0.0068	-2.0423	-3.1825
Eudorcas thomsoni	Plains	MT	6	0.0445	0.0676	0.0162	-0.1056	-1.5838	-1.7587
				(0.0139)	(0.0091)	(0.0115)	(0.0704)	(0.2987)	(0.3258)
		MC	6	0.0697	-0.027	-0.0002	-0.0106	-0.5634	-1.8626
				(0.0091)	(0.0286)	(0.0204)	(0.0155)	(0.3485)	(0.4091)
Gazella gazella	Plains	MT	1	0.0432	0.0928	0.032	0.0378	-2.0901	-1.8976
		MC	1	0.0537	0.0007	0.0192	0.0242	-1.0045	-1.9842
Litocranius walleri	Light cover	MT	5	0.1332	0.0649	0.0149	-0.0294	-2.3924	-2.2479
				(0.0065)	(0.0086)	(0.0089)	(0.0314)	(0.5515)	(0.4836)
		MC	5	0.2144	-0.01	-0.0021	-0.0192	-1.9136	-2.3295
				(0.0075)	(0.0065)	(0.0194)	(0.0137)	(0.3641)	(0.7165)
Nanger granti	Plains	MT	9	0.0955	0.0754	0.009	-0.0842	-2.1009	-1.9127
				(0.0056)	(0.009)	(0.0069)	(0.0506)	(0.3487)	(0.4308)
		MC	9	0.1105	-0.0237	-0.0041	-0.0135	-1.2941	-2.2589
				(0.0065)	(0.0066)	(0.0069)	(0.0157)	(0.4801)	(0.7826)
Nanger soemmerringi	Plains	MT	2	0.0684	0.0756	0.0208	-0.0276	-1.5203	-1.5198
				(0.0011)	(0.008)	(0.0031)	(0.0114)	(0.3681)	(0.2206)
		MC	2	0.0761	-0.0173	-0.0015	-0.04	-0.8392	-2.664
				(0.004)	(0.004)	(0.0143)	(0.0004)	(0.5439)	(1.2238)
Neotragini									
Madoqua guentheri	Heavy cover	MT	3	-0.0055	0.0735	0.0145	-0.0086	-0.3843	-0.525
				(0.0177)	(0.0125)	(0.0105)	(0.069)	(0.4625)	(0.25)
		MC	3	-0.0199	0.0039	0.023	-0.0238	0.1893	-0.7014
				(0.0182)	(0.0136)	(0.0051)	(0.0071)	(0.6971)	(0.3455)
Madoqua kirki	Heavy cover	MT	6	-0.0421	0.0785	0.0034	0.0027	0.5408	0.286
				(0.0079)	(0.0127)	(0.0106)	(0.0361)	(0.4577)	(0.4278)
		MC	6	-0.0475	0.0107	0.0098	-0.0264	-0.0296	-0.8159
				(0.0065)	(0.0112)	(0.012)	(0.0196)	(0.1689)	(0.2689)

Madoqua sp.	Heavy cover	MT	3	-0.0316	0.0975	-0.0017	0.0003	0.1269	-0.1069
				(0.0132)	(0.0044)	(0.0182)	(0.0596)	(1.0563)	(1.0126)
		MC	3	-0.0508	0.0117	0.0066	-0.0303	0.6825	-0.3193
				(0.0084)	(0.0152)	(0.0095)	(0.0153)	(0.6675)	(0.5118)
Neotragus batesi	Forest	MT	1	0.0056	0.0644	0.0019	0.0979	0.946	0.3722
		MC	1	-0.1181	0.0266	0.0397	-0.0757	0.8546	-0.016
Nesotragus moschatus	Forest	MT	1	-0.0668	0.0799	0.0024	0.1141	2.47	2.1291
		MC	1	-0.1658	0.03	0.0055	-0.0275	1.0812	1.0578
Oreotragus oreotragus	Mountain	MT	7	-0.1477	0.0713	-0.0393	-0.1355	1.7711	0.4794
				(0.0093)	(0.0092)	(0.0168)	(0.1198)	(0.5385)	(0.3472)
		MC	7	-0.1581	-0.0089	-0.0413	-0.0445	2.9885	-0.3854
				(0.0117)	(0.0071)	(0.0097)	(0.0204)	(0.5708)	(0.7274)
Ourebia ourebi	Light cover	MT	7	0.0101	0.0798	0.0184	0.005	-0.9372	-1.0502
				(0.0148)	(0.0135)	(0.0172)	(0.0386)	(0.7009)	(0.7051)
		MC	7	0.0568	0.0121	0.0009	-0.0081	-0.6868	-1.3228
				(0.016)	(0.0156)	(0.0193)	(0.0257)	(0.4115)	(0.528)
Raphicerus campestris	Light cover	MT	5	-0.0133	0.0833	-0.0001	0.0192	-0.4064	-0.3779
				(0.0155)	(0.0102)	(0.0106)	(0.1003)	(0.5518)	(0.5671)
		MC	5	0.0144	0.0181	0.0065	-0.0096	-0.1689	-0.9756
				(0.0213)	(0.0049)	(0.0123)	(0.0215)	(0.6558)	(0.9974)
Raphicerus sharpei	Light cover	MT	1	-0.0956	0.0853	-0.0358	-0.1278	0.9524	0.6388
		MC	1	-0.0865	0.0104	-0.0314	-0.0193	0.6874	-0.4363
Saigini									
Saiga tatarica	Plains	MT	3	0.0437	0.0901	0.0191	-0.1185	-2.6042	-2.7529
				(0.0023)	(0.0073)	(0.002)	(0.086)	(0.341)	(0.3358)

		MC	3	-0.0041	0.0074	-0.0134	0.0057	-1.0488	-2.6391
				(0.0034)	(0.0059)	(0.011)	(0.0383)	(0.2837)	(0.1026)
Bovinae									
Boselaphini									
Boselaphus tragocamelus	Heavy cover	MT	5	0.0077	0.0863	0.0153	-0.1729	0.9515	0.7774
				(0.0086)	(0.0189)	(0.0199)	(0.045)	(0.7645)	(0.7443)
		MC	6	0.0425	0.0049	-0.0168	-0.041	-0.0421	0.141
				(0.0072)	(0.023)	(0.0057)	(0.0224)	(0.8379)	(0.9883)
Tetracerus quadricornis	Heavy cover	MT	4	0.0044	0.0899	-0.0137	-0.0406	0.6027	0.8491
				(0.0246)	(0.0414)	(0.0045)	(0.1222)	(0.8057)	(0.9418)
		MC	3	0.0007	0.0033	-0.0213	-0.0467	-0.0429	1.0323
				(0.0317)	(0.0089)	(0.0175)	(0.0376)	(0.739)	(0.9181)
Bovini									
Anoa depressicornis	Forest	MT	6	-0.166	0.123	-0.019	0.1045	1.8242	1.7208
				(0.0135)	(0.0063)	(0.0172)	(0.0497)	(0.5608)	(0.4796)
		MC	6	-0.2056	0.0385	-0.022	-0.0097	1.4388	1.3036
				(0.0217)	(0.0098)	(0.0116)	(0.0195)	(0.443)	(0.7222)
Anoa mindorensis	Forest	MT	2	-0.1869	0.1105	-0.0642	-0.0988	2.7777	2.3032
				(0.0227)	(0.0015)	(0.0007)	(0.0388)	(0.9406)	(0.8218)
		MC	2	-0.2376	-0.003	-0.0211	-0.0696	1.7558	0.7952
				(0.0314)	(0.0019)	(0.008)	(0.0104)	(0.7891)	(0.177)
Bison bison athabaskae	Light cover	MT	5	-0.0567	0.0986	-0.0049	-0.0193	0.285	-0.0499
				(0.0106)	(0.0199)	(0.0155)	(0.0484)	(0.5678)	(0.4888)
		MC	5	-0.1087	0.0406	0.0077	-0.016	0.7779	-0.0428
				(0.0162)	(0.0151)	(0.0078)	(0.016)	(0.3612)	(0.4774)
Bison bison bison	Plains	MT	6	-0.0709	0.0882	-0.0092	0.0014	0.0812	-0.0856
				(0.0161)	(0.0172)	(0.0134)	(0.0755)	(0.6486)	(0.6043)
		MC	5	-0.1315	0.0295	0.0043	-0.0171	0.0754	-0.3307
				(0.0106)	(0.013)	(0.01)	(0.0165)	(0.4061)	(0.7368)
Bos gaurus	Heavy cover	MT	5	-0.0467	0.0881	-0.0059	0.0382	1.0968	1.033
				(0.0132)	(0.0104)	(0.0096)	(0.0773)	(0.2724)	(0.1905)

		MC	5	-0.0569	0.0305	-0.0097	-0.0169	1.2895	1.2266
				(0.0196)	(0.0106)	(0.0076)	(0.0114)	(0.2629)	(0.3301)
Bos grunniens	Mountain	MT	4	-0.1308	0.1011	-0.017	-0.119	1.7192	0.9703
				(0.0137)	(0.0258)	(0.015)	(0.2377)	(0.4514)	(0.4339)
		MC	4	-0.1908	0.0437	-0.0183	-0.0071	2.3674	0.8318
				(0.0148)	(0.0162)	(0.0075)	(0.0197)	(0.4323)	(0.7478)
Bos sauveli	Heavy cover	MT	2	-0.0252	0.0798	0.0062	0.0955	-0.4103	-0.2052
				(0.0004)	(0.0011)	(0.0012)	(0.1027)	(0.2676)	(0.4408)
		MC	2	-0.0412	0.0217	0.0082	-0.0179	0.0237	0.9075
				(0.0068)	(0.0106)	(0.014)	(0.0147)	(0.4787)	(0.6413)
Bubalis bubalis	Heavy cover	MT	1	-0.1041	0.1258	-0.0088	0.109	-0.0153	-0.0063
		MC	1	-0.1447	0.0585	-0.004	-0.0515	0.4284	-0.5289
Syncerus caffer caffer	Light cover	MT	3	-0.1467	0.1039	-0.0191	0.1475	2.4361	2.0755
				(0.0099)	(0.0127)	(0.0162)	(0.0394)	(0.554)	(0.6139)
		MC	3	-0.1786	0.0176	-0.0196	-0.0328	2.1671	1.0618
				(0.0088)	(0.0167)	(0.0164)	(0.0071)	(0.3543)	(0.6771)
Syncerus caffer nanus	Heavy cover	MT	3	-0.1398	0.105	-0.0068	0.1628	1.4724	0.9122
				(0.008)	(0.0155)	(0.0081)	(0.0339)	(0.1448)	(0.48)
		MC	3	-0.1668	0.0236	-0.011	-0.0371	1.484	0.4583
				(0.0106)	(0.0127)	(0.0118)	(0.0236)	(0.5068)	(0.6628)
Tragelaphini									
Tragelaphus angasi	Heavy cover	MT	1	0.0803	0.0987	-0.0206	0.0623	0.9467	1.2975
		MC	1	0.0985	-0.0193	-0.0006	-0.0931	-1.7871	-0.6194
Tragelaphus derbianus	Light cover	MT	1	0.0269	0.0829	-0.0044	0.1995	0.8329	1.0207
		MC	1	0.0443	0.0117	0.0115	-0.0469	-0.0152	0.1068

Tragelaphus eurycerus	Forest	MT	9	-0.0509	0.0903	-0.0022	0.0557	3.2374	3.3688
				(0.0131)	(0.0108)	(0.0136)	(0.0668)	(0.6626)	(0.6387)
		MC	9	-0.0455	-0.0507	0.0519	-0.0716	1.6483	1.9461
				(0.0109)	(0.0879)	(0.0909)	(0.017)	(0.4247)	(0.625)
Tragelaphus imberbis	Heavy cover	MT	5	0.1201	0.0613	0.0052	0.0581	0.7931	1.3716
				(0.0061)	(0.0089)	(0.008)	(0.0694)	(0.2266)	(0.2311)
		MC	5	0.1436	-0.0248	-0.0138	-0.0671	-1.3367	0.0924
				(0.0078)	(0.003)	(0.0133)	(0.028)	(0.3044)	(0.4824)
Tragelaphus oryx	Light cover	MT	6	0.0144	0.0939	0.0066	0.0312	0.1754	0.1476
				(0.0121)	(0.0174)	(0.0106)	(0.0658)	(0.9079)	(0.9385)
		MC	6	0.0085	0.007	0.0005	-0.0499	-0.4538	-0.2011
				(0.014)	(0.024)	(0.0077)	(0.0154)	(1.219)	(1.553)
Tragelaphus scriptus	Forest	MT	14	0.025	0.0853	-0.0137	0.1239	1.7055	2.1261
				(0.0079)	(0.011)	(0.0526)	(0.068)	(0.7738)	(0.7249)
		MC	15	0.034	-0.0149	-0.0063	-0.0773	0.2724	1.381
				(0.0106)	(0.0102)	(0.0214)	(0.024)	(0.4926)	(0.5963)
Tragelaphus spekei	Heavy cover	MT	6	0.0458	0.0715	-0.0111	0.1573	1.5614	1.8397
				(0.0119)	(0.0142)	(0.0162)	(0.0356)	(0.6437)	(0.7354)
		MC	6	0.0459	-0.0389	0.0097	-0.0793	1.17	2.2931
				(0.0087)	(0.0679)	(0.0786)	(0.0212)	(0.4931)	(0.4466)
Tragelaphus strepsiceros	Heavy cover	MT	7	0.0928	0.0789	0.0105	0.0187	0.5258	0.8679
				(0.0288)	(0.0164)	(0.0153)	(0.0733)	(0.4809)	(0.2134)
		MC	6	0.1145	-0.0175	0.005	-0.0481	-0.0721	0.8464
				(0.0345)	(0.0121)	(0.0181)	(0.0156)	(0.4991)	(0.5925)
Caprinae									
Caprini									
Ammotragus lervia	Mountain	MT	4	-0.0686	0.0864	-0.0215	-0.0162	1.9936	0.7741
				(0.0243)	(0.0246)	(0.011)	(0.1296)	(0.5516)	(0.7616)
		MC	4	-0.0759	-0.0257	0.0271	-0.1053	2.0309	-1.4057
				(0.0161)	(0.0579)	(0.0391)	(0.1804)	(0.2262)	(1.0072)

Ovis ammon	Mountain	MT	5	0.0333	0.0663	0.0056	-0.0397	-0.4849	-1.4601
				(0.0152)	(0.0057)	(0.0073)	(0.0728)	(0.4991)	(0.5671)
		MC	5	0.0283	-0.0128	0.0124	-0.0399	0.1562	-2.3082
				(0.0167)	(0.0082)	(0.0101)	(0.0134)	(0.3635)	(0.6617)
Pantholopini									
Pantholops hodgsoni	Plains	MT	1	0.0572	0.0833	0.0303	-0.0528	-3.0988	-3.2529
		MC	1	0.0285	-0.0003	0.0389	0.0163	-2.3471	-3.1641
Rupicaprini									
Budorcas taxicolor	Mountain	MT	1	-0.2342	0.062	-0.0237	-0.1038	4.5333	2.6757
		MC	1	-0.2774	-0.0011	-0.0137	-0.0411	4.6244	0.569
Myotragus balearicus	Mountain	MT	1	-0.3936	0.1223	-0.0743	.	6.5819	5.9766
		MC	1	-0.4608	-0.0183	-0.0461	-0.062	4.9882	2.1334
Naemorhedus crispus	Mountain	MT	1	-0.1175	0.109	-0.0301	-0.0305	1.0217	-0.7541
		MC	1	-0.1404	0.0284	-0.0271	-0.0555	3.5215	-0.5946
Naemorhedus goral	Mountain	MT	7	-0.1035	0.1221	-0.0183	0.038	0.1748	-0.8416
				(0.0088)	(0.0206)	(0.0171)	(0.0679)	(0.4492)	(0.6428)
		MC	7	-0.1308	0.0258	0.0069	-0.0223	2.2675	-0.2746
				(0.0098)	(0.0077)	(0.0156)	(0.0223)	(0.7294)	(0.4523)
Naemorhedus sumatraensis	Mountain	MT	5	-0.0737	0.1073	-0.0271	0.0476	1.4347	0.2317
				(0.0129)	(0.0094)	(0.0207)	(0.0657)	(0.3747)	(0.327)
		MC	5	-0.0719	0.008	-0.009	-0.0922	3.4608	0.3831
				(0.0117)	(0.0079)	(0.01)	(0.0459)	(0.4032)	(0.9676)

Naemorhedus swinhoei	Mountain	MT	1	-0.1474	0.1162	-0.0391	-0.1387	1.9907	0.429
		MC	1	-0.1832	0.0155	-0.0105	0.0055	4.2168	0.4778
Oreamnos americanus	Mountain	MT	3	-0.2124	0.1006	-0.0478	0.0081	2.8738	0.9622
				(0.0101)	(0.0037)	(0.0174)	(0.0326)	(0.346)	(0.2322)
		MC	3	-0.2424	0.0108	-0.0062	-0.0412	6.0995	0.4902
				(0.009)	(0.015)	(0.0151)	(0.0105)	(0.2394)	(0.227)
Rupicapra rupicapra	Mountain	MT	1	-0.0167	0.0725	-0.0195	-0.0142	-1.12	-2.9501
		MC	1	-0.0538	-0.012	0.0025	-0.0013	2.6257	-1.6997
Cephalophinae									
Cephalophini									
Cephalophus dorsalis	Forest	MT	5	-0.105	0.1007	-0.016	0.1125	2.7853	2.9602
				(0.0103)	(0.0082)	(0.0107)	(0.128)	(0.2422)	(0.1879)
		MC	5	-0.1409	0.0211	-0.0165	-0.0206	1.0627	1.986
				(0.0287)	(0.0071)	(0.0058)	(0.0274)	(0.3078)	(0.6344)
Cephalophus leucogaster	Forest	MT	5	-0.0557	0.0979	0.0084	0.1154	1.4185	1.6705
				(0.0086)	(0.0155)	(0.0133)	(0.0479)	(0.3692)	(0.1721)
		MC	5	-0.0896	0.0349	0.0115	-0.0084	-0.3967	0.9018
				(0.0108)	(0.0194)	(0.0149)	(0.0396)	(0.7182)	(0.6766)
Cephalophus sylvicultor	Forest	MT	7	-0.0645	0.1018	-0.0265	0.1169	2.4128	2.3073
				(0.006)	(0.0166)	(0.0186)	(0.0848)	(0.5437)	(0.5434)
		MC	7	-0.0665	0.0006	0.0042	-0.0163	1.0252	0.7278
				(0.0131)	(0.0118)	(0.0115)	(0.011)	(0.7315)	(0.6738)
Cephalophus weynsi	Forest	MT	1	-0.0638	0.1044	-0.0134	0.2268	1.4534	1.626
		MC	1	-0.1203	0.0192	0.0219	-0.0556	0.4708	0.6946

Philantomba monticola	Forest	MT	1	-0.0384	0.0898	0.0228	0.1339	3.0809	3.4819
		MC	1	-0.1312	0.035	0.0244	-0.015	0.3929	1.2366
Sylvicapra grimmia	Light cover	MT	7	0.0033	0.1007	0.0093	0.0172	0.5156	1.01
				(0.0248)	(0.0202)	(0.0102)	(0.0621)	(0.6894)	(0.7219)
		MC	9	-0.0237	0.016	0.0083	-0.0403	-0.5848	0.4991
				(0.0296)	(0.0144)	(0.0169)	(0.0234)	(0.8204)	(0.5141)
Hippotraginae									
Hippotragini									
Addax nasomaculatus	Plains	MT	4	0.0091	0.0866	0.0136	0.0151	-2.7065	-2.971
				(0.0113)	(0.0087)	(0.0111)	(0.0209)	(0.2762)	(0.326)
		MC	4	-0.0243	0.0082	-0.0027	-0.0087	-0.961	-2.3741
				(0.0074)	(0.0074)	(0.0076)	(0.0066)	(0.5129)	(0.5257)
Hippotragus equinus	Light cover	MT	5	0.0351	0.1034	0.0181	-0.0196	-1.0486	-1.2014
				(0.0188)	(0.0131)	(0.0129)	(0.1186)	(0.5054)	(0.566)
		MC	5	0.0585	-0.0015	0.016	-0.003	-1.1922	-1.7003
				(0.0157)	(0.0168)	(0.0064)	(0.0265)	(0.7048)	(0.6959)
Hippotragus niger	Light cover	MT	6	0.0062	0.0702	0.0032	-0.0327	-0.5615	-0.7705
				(0.0151)	(0.0685)	(0.0112)	(0.0624)	(0.5771)	(0.591)
		MC	6	0.0306	0.0109	0.0076	-0.0162	-0.3477	-0.3533
				(0.0159)	(0.0095)	(0.0115)	(0.0119)	(1.3431)	(1.6115)
Oryx beisa	Plains	MT	2	-0.0021	0.1087	0.0121	-0.0132	-1.4617	-1.7327
				(0.0085)	(0.0053)	(0.0024)	(0.0157)	(0.2496)	(0.2346)
		MC	2	0.0045	0.0251	0.0065	-0.0021	-0.7428	-1.4771
				(0.0025)	(0.025)	(0.0116)	(0.0083)	(0.1566)	(0.2953)
Oryx dammah	Plains	MT	2	0.0284	0.09	0.0115	0.0005	-1.9215	-1.8343
				(0.0042)	(0.0161)	(0.0315)	(0.036)	(0.2263)	(0.3061)
		MC	2	0.0289	0.0199	0.0053	0.0012	-0.8704	-1.3965
				(0.0016)	(0.0007)	(0.0003)	(0.0231)	(0.5949)	(0.8218)

Oryx gazella	Plains	MT	2	0.0118	0.0977	0.0048	-0.1896	-1.043	-1.482
				(0.0166)	(0.0034)	(0.0099)	(0.0695)	(0.9427)	(0.8051)
		MC	2	0.0238	0.0051	-0.0077	-0.0028	-0.3936	-1.6232
				(0.0084)	(0.0021)	(0.0064)	(0.0036)	(0.7737)	(0.4815)
Oryx leucoryx	Plains	MT	1	0.017	0.1139	0.0214	0.0089	-2.3507	-2.7274
		MC	1	0.027	0.0457	-0.0085	0.0333	-1.6257	-3.4243
Reduncinae									
Reduncini									
Kobus ellipsiprymnus	Heavy cover	MT	7	-0.0102	0.0955	0.0015	-0.0884	0.0356	-0.129
				(0.016)	(0.0263)	(0.0088)	(0.0875)	(0.4518)	(0.5458)
		MC	8	0.0324	0.0077	-0.0048	-0.0105	-0.1017	-0.9243
				(0.0191)	(0.0134)	(0.0136)	(0.0125)	(0.5983)	(0.4597)
Kobus kob	Light cover	MT	9	0.0083	0.0791	0.0038	0.0083	-1.0255	-1.1073
				(0.0122)	(0.0113)	(0.0083)	(0.038)	(0.5246)	(0.483)
		MC	9	0.0353	-0.0116	0.0022	-0.0218	-0.4581	-0.5401
				(0.0118)	(0.0105)	(0.0116)	(0.0219)	(0.3765)	(0.59)
Kobus leche	Light cover	MT	1	0.0483	0.0827	0.001	0.0019	-1.6694	-1.9362
		MC	1	0.0765	-0.013	0.0111	-0.0197	-0.2337	0.2089
Kobus megaceros	Heavy cover	MT	6	0.0261	0.0744	0.001	-0.0359	-0.5464	-0.6409
				(0.0306)	(0.0112)	(0.02)	(0.0662)	(0.4985)	(0.6234)
		MC	6	0.0469	-0.0116	0.0079	-0.0242	-0.4657	-0.6014
				(0.02)	(0.009)	(0.0186)	(0.0228)	(0.7092)	(0.5875)
Redunca arundinum	Light cover	MT	5	0.1001	0.0667	0.0164	0.0102	-1.1661	-0.8393
				(0.0162)	(0.0091)	(0.0085)	(0.081)	(0.3725)	(0.4621)
		MC	5	0.1246	-0.0201	0.0123	-0.0341	-0.8559	-0.4
				(0.0165)	(0.0103)	(0.0112)	(0.0096)	(0.3536)	(0.4735)

Redunca fulvorufula	Light cover	MT	7	0.0467	0.0788	-0.0065	0.0223	-0.435	-0.6465
				(0.0063)	(0.0126)	(0.0108)	(0.0681)	(0.4796)	(0.6332)
		MC	7	0.0577	-0.0089	-0.0049	-0.0301	0.0117	-0.5673
				(0.0056)	(0.0125)	(0.0097)	(0.0215)	(0.193)	(0.3384)
Redunca redunca	Light cover	MT	5	0.0743	0.0726	0.009	-0.1571	-0.0753	-0.0292
				(0.0217)	(0.0092)	(0.0172)	(0.0883)	(0.6279)	(0.5617)
		MC	5	0.1009	-0.0139	0.003	-0.0565	-0.5563	-0.1288
				(0.0183)	(0.0116)	(0.011)	(0.0192)	(0.4747)	(0.7201)

Table A3: Summary by species of diaphyseal variables based on analysis of complete metapodials.

Species	Habitat	Elem.	*N*	MML	MAP	PQML	PQAP	DQML	DQAP	DDML	DDAP
Antilocapridae											
Antilocaprinae											
Antilocaprini											
Antilocapra americana	Plains	MT	11	-0.0187	-0.1179	-0.1413	-0.0507	-0.0572	-0.0476	-0.0062	-0.0476
				(0.0201)	(0.0198)	(0.0186)	(0.0233)	(0.012)	(0.009)	(0.0084)	(0.0154)
		MC	6	-0.0323	-0.0025	-0.0521	-0.1112	-0.0846	-0.2133	-0.0101	-0.0327
				(0.0169)	(0.0253)	(0.0142)	(0.0315)	(0.0208)	(0.0253)	(0.0094)	(0.0109)
Bovidae											
Aepycerotinae											
Aepycerotini											
Aepyceros melampus	Light cover	MT	11	-0.0279	-0.0681	-0.1522	-0.0264	-0.0287	-0.0276	-0.0282	-0.0381
				(0.0255)	(0.0189)	(0.0204)	(0.0183)	(0.0112)	(0.0106)	(0.0136)	(0.0251)
		MC	11	-0.0226	0.025	-0.0272	-0.1019	-0.0408	-0.1913	-0.0219	-0.013
				(0.0175)	(0.0112)	(0.0166)	(0.0183)	(0.0152)	(0.0165)	(0.0079)	(0.0174)
Alcelaphinae											
Alcelaphini											
Alcelaphus buselaphus	Plains	MT	9	-0.0204	-0.0756	-0.1261	-0.0297	-0.0396	-0.0011	-0.011	-0.0186
				(0.0216)	(0.0157)	(0.0474)	(0.0325)	(0.0251)	(0.0175)	(0.0109)	(0.0164)
		MC	9	-0.0286	0.0023	-0.038	-0.1333	-0.0375	-0.1801	-0.0135	-0.02
				(0.0197)	(0.0141)	(0.0162)	(0.0176)	(0.0247)	(0.0275)	(0.0142)	(0.0214)
Alcelaphus lichtensteini	Plains	MT	1	-0.0108	-0.0869	-0.1264	-0.0404	-0.0152	-0.0304	-0.0043	-0.0283
		MC	1	-0.0216	-0.007	-0.0247	-0.1339	-0.0312	-0.2127	-0.017	-0.0205
Beatragus hunteri	Plains	MT	3	-0.044	-0.0597	-0.069	0.0345	-0.0773	0.0078	-0.0217	0.0092
				(0.003)	(0.0072)	(0.1336)	(0.0684)	(0.013)	(0.0083)	(0.0035)	(0.0057)

		MC	3	-0.0444	0.0055	-0.0294	-0.1263	-0.0523	-0.1908	-0.0124	0.0154
				(0.0024)	(0.009)	(0.0093)	(0.0079)	(0.0062)	(0.0034)	(0.0066)	(0.0041)
Connochaetes gnou	Plains	MT	4	-0.0239	-0.1166	-0.155	-0.0538	-0.0341	-0.0342	-0.002	-0.0265
				(0.0142)	(0.0193)	(0.0097)	(0.0205)	(0.0457)	(0.0116)	(0.0107)	(0.0221)
		MC	4	-0.0447	-0.0308	-0.0189	-0.168	-0.0018	-0.2025	0.0047	-0.0383
				(0.0193)	(0.0092)	(0.0233)	(0.0168)	(0.0333)	(0.0121)	(0.0037)	(0.0104)
Connochaetes taurinus	Plains	MT	6	-0.0095	-0.0961	-0.1394	-0.0275	-0.0238	-0.0298	0.0092	-0.0556
				(0.0097)	(0.0139)	(0.0102)	(0.0171)	(0.0038)	(0.0077)	(0.0098)	(0.0175)
		MC	6	-0.0102	-0.0202	-0.0221	-0.1506	-0.0125	-0.2232	0.0102	-0.0498
				(0.0332)	(0.0149)	(0.0111)	(0.0184)	(0.0126)	(0.0129)	(0.0075)	(0.0176)
Damaliscus dorcas	Plains	MT	5	-0.0444	-0.0793	-0.1724	-0.0175	-0.0535	0.0044	-0.0144	-0.0169
				(0.0114)	(0.0099)	(0.0147)	(0.0156)	(0.0129)	(0.0098)	(0.0093)	(0.0188)
		MC	5	-0.0543	0.0037	-0.0607	-0.1075	-0.0466	-0.1812	-0.0175	-0.005
				(0.0162)	(0.0059)	(0.0172)	(0.0078)	(0.0146)	(0.0114)	(0.01)	(0.0249)
Damaliscus lunatus	Plains	MT	7	-0.0284	-0.0837	-0.1474	-0.0209	-0.0406	-0.0086	-0.0035	-0.0001
				(0.0144)	(0.0136)	(0.0115)	(0.0151)	(0.0339)	(0.0129)	(0.0108)	(0.0112)
		MC	7	-0.0421	0.0013	-0.0473	-0.1264	-0.0534	-0.1878	-0.0146	-0.0104
				(0.0141)	(0.0168)	(0.0138)	(0.0176)	(0.0254)	(0.0161)	(0.0109)	(0.0149)
Antilopinae											
Antilopini											
Antidorcas marsupialis	Plains	MT	5	-0.0589	-0.059	-0.1825	-0.0087	-0.0666	0.0105	-0.0156	-0.0058
				(0.0246)	(0.0093)	(0.0207)	(0.0114)	(0.0316)	(0.0218)	(0.0093)	(0.0129)
		MC	5	-0.0404	0.0083	-0.0405	-0.109	-0.0583	-0.1981	-0.0221	-0.0472
				(0.021)	(0.0157)	(0.0215)	(0.0152)	(0.0386)	(0.0249)	(0.0145)	(0.0132)
Antilope cervicapra	Plains	MT	3	-0.0529	-0.096	-0.1527	-0.0459	-0.0773	-0.0334	0.0027	-0.0017
				(0.0134)	(0.0196)	(0.0023)	(0.0254)	(0.0567)	(0.0253)	(0.013)	(0.0443)
		MC	3	-0.0305	-0.0133	-0.0132	-0.1262	-0.0772	-0.2223	-0.0025	-0.0307
				(0.0118)	(0.0273)	(0.0036)	(0.0225)	(0.0715)	(0.0509)	(0.0125)	(0.0405)

Eudorcas rufifrons	Plains	MT	1	-0.0446	-0.0917	-0.1488	-0.0442	-0.0276	-0.0277	-0.003	0.005
		MC	1	-0.031	-0.0277	-0.0422	-0.1495	-0.0255	-0.1902	-0.0119	-0.0216
Eudorcas thomsoni	Plains	MT	6	-0.0467	-0.0628	-0.1724	-0.0209	-0.0396	-0.0166	-0.0031	-0.0136
				(0.0117)	(0.0092)	(0.0091)	(0.0097)	(0.0152)	(0.0083)	(0.0096)	(0.017)
		MC	6	-0.0226	0.0098	-0.0267	-0.1088	-0.0155	-0.1859	-0.0049	0.0015
				(0.0172)	(0.0129)	(0.0076)	(0.0136)	(0.0151)	(0.0149)	(0.0078)	(0.0202)
Gazella gazella	Plains	MT	1	-0.0736	-0.069	-0.1776	-0.0188	-0.1053	-0.0248	-0.0007	-0.0042
		MC	1	-0.028	-0.0195	-0.0113	-0.1375	-0.0686	-0.235	-0.012	-0.0156
Litocranius walleri	Light cover	MT	5	-0.0301	-0.0511	-0.1646	-0.02	-0.0684	0.0168	-0.0346	0.011
				(0.0154)	(0.0068)	(0.018)	(0.0109)	(0.0228)	(0.0099)	(0.0041)	(0.0194)
		MC	5	-0.0378	0.0407	-0.0454	-0.0966	-0.0781	-0.1593	-0.041	-0.0084
				(0.0216)	(0.0204)	(0.0221)	(0.0175)	(0.025)	(0.0109)	(0.0079)	(0.0226)
Nanger granti	Plains	MT	9	-0.0467	-0.0615	-0.1587	-0.016	-0.0675	0.0081	-0.022	0.0125
				(0.0143)	(0.0157)	(0.0121)	(0.0162)	(0.0245)	(0.0081)	(0.0107)	(0.0162)
		MC	9	-0.0403	0.0179	-0.0387	-0.1191	-0.0348	-0.1566	-0.0263	0.0056
				(0.0159)	(0.0199)	(0.0252)	(0.0137)	(0.0629)	(0.0459)	(0.0105)	(0.0277)
Nanger soemmerringi	Plains	MT	2	-0.0494	-0.0596	-0.1824	-0.0212	-0.041	-0.0001	-0.0137	-0.0142
				(0.0144)	(0.0134)	(0.0028)	(0.0204)	(0.013)	(0.006)	(0.0002)	(0.0135)
		MC	2	-0.0461	0.0194	-0.0354	-0.1029	-0.0389	-0.1854	-0.0194	-0.0277
				(0.0094)	(0.0048)	(0.0013)	(0.0011)	(0.0308)	(0.0015)	(0.0035)	(0.0131)
Neotragini											
Madoqua guentheri	Heavy cover	MT	3	-0.02	-0.1023	-0.1148	-0.0554	0.0161	-0.0059	-0.0011	0.0002
				(0.0186)	(0.0125)	(0.008)	(0.02)	(0.0194)	(0.0362)	(0.0069)	(0.0195)
		MC	3	-0.015	-0.0219	0.0126	-0.1373	-0.0094	-0.2147	0.0172	0.0037
				(0.008)	(0.0169)	(0.0114)	(0.0219)	(0.0408)	(0.0242)	(0.0038)	(0.0241)

Madoqua kirki	Heavy cover	MT	6	0.012	-0.1031	-0.1059	-0.0676	0.024	-0.0141	0.0046	-0.0044
				(0.0136)	(0.0095)	(0.0157)	(0.01)	(0.0261)	(0.0063)	(0.0097)	(0.0151)
		MC	6	0.0128	-0.0229	0.0319	-0.1384	0.0321	-0.1988	0.0076	-0.0166
				(0.0155)	(0.0115)	(0.0151)	(0.0069)	(0.0224)	(0.0191)	(0.0072)	(0.0271)
Madoqua sp.	Heavy cover	MT	3	-0.0172	-0.0871	-0.1234	-0.0468	0.0177	-0.0011	-0.0023	0.0196
				(0.0179)	(0.0232)	(0.0241)	(0.0158)	(0.0073)	(0.0084)	(0.017)	(0.0358)
		MC	3	-0.0001	-0.004	0.0233	-0.1278	0.0356	-0.1757	0.0074	0.0108
				(0.0228)	(0.0038)	(0.0224)	(0.0103)	(0.0317)	(0.0233)	(0.0037)	(0.008)
Neotragus batesi	Forest	MT	1	0.0212	-0.118	-0.0638	-0.0566	-0.0019	-0.0084	0.0336	-0.0271
		MC	1	-0.0113	-0.0418	0.0522	-0.1316	-0.0131	-0.2239	0.0251	-0.0312
Nesotragus moschatus	Forest	MT	1	0.0432	-0.1365	-0.0667	-0.081	0.0503	-0.0364	0.0376	-0.0062
		MC	1	0.0415	-0.0601	0.055	-0.1693	0.0647	-0.2406	0.0355	-0.0196
Oreotragus oreotragus	Mountain	MT	7	0.0201	-0.1303	-0.1308	-0.1	0.0745	-0.0017	0.0227	0.0101
				(0.0137)	(0.0194)	(0.0207)	(0.0255)	(0.0232)	(0.0188)	(0.0151)	(0.0181)
		MC	7	0.0567	-0.0461	0.0341	-0.1785	0.0916	-0.1883	0.0575	-0.0021
				(0.0206)	(0.0183)	(0.0153)	(0.0187)	(0.0223)	(0.0223)	(0.0093)	(0.0346)
Ourebia ourebi	Light cover	MT	7	-0.0128	-0.0883	-0.1539	-0.0374	-0.0173	-0.0053	-0.0079	0.0053
				(0.0196)	(0.0152)	(0.0205)	(0.0131)	(0.0257)	(0.0162)	(0.0099)	(0.0212)
		MC	7	-0.0085	-0.0039	-0.0196	-0.1298	-0.0016	-0.1937	-0.0133	0.0152
				(0.0168)	(0.0151)	(0.0175)	(0.0118)	(0.0311)	(0.0216)	(0.0101)	(0.0132)
Raphicerus campestris	Light cover	MT	5	-0.0048	-0.0872	-0.126	-0.0528	-0.009	0.0284	0.0062	0.0556
				(0.0118)	(0.0141)	(0.0204)	(0.0103)	(0.0261)	(0.0079)	(0.0068)	(0.0527)
		MC	5	-0.0013	-0.0177	-0.0178	-0.1344	-0.0071	-0.114	0.0007	0.0141
				(0.0158)	(0.0063)	(0.0171)	(0.0153)	(0.0164)	(0.1814)	(0.0122)	(0.0276)

Raphicerus sharpei	Light cover	MT	1	0.0244	-0.0739	-0.1002	-0.0658	0.0246	0.0431	0.0002	0.0063
		MC	1	0.0503	-0.0204	0.0553	-0.1209	0.0374	-0.1708	0.0029	-0.0007
Saigini											
Saiga tatarica	Plains	MT	3	-0.0545	-0.076	-0.1826	-0.0138	-0.0378	-0.0102	0.0028	-0.0226
				(0.0066)	(0.0099)	(0.0022)	(0.016)	(0.0268)	(0.0095)	(0.0047)	(0.022)
		MC	3	-0.0415	0.0134	-0.0635	-0.1047	-0.0254	-0.219	0.0089	-0.0125
				(0.0154)	(0.0194)	(0.0201)	(0.0035)	(0.0293)	(0.0054)	(0.008)	(0.0011)
Bovinae											
Boselaphini											
Boselaphus tragocamelus	Heavy cover	MT	5	-0.0049	-0.1117	-0.1225	-0.0455	-0.0185	-0.0044	-0.0265	0.0386
				(0.0229)	(0.0107)	(0.0187)	(0.0135)	(0.0133)	(0.0128)	(0.02)	(0.0197)
		MC	6	-0.0201	-0.0286	-0.0271	-0.1536	-0.0313	-0.169	-0.0259	0.0663
				(0.0239)	(0.0157)	(0.0093)	(0.0267)	(0.0265)	(0.0127)	(0.0138)	(0.0147)
Tetracerus quadricornis	Heavy cover	MT	4	0.0141	-0.0923	-0.1202	-0.0398	-0.0056	-0.0127	-0.0013	0.0349
				(0.0243)	(0.029)	(0.0154)	(0.0306)	(0.0464)	(0.0379)	(0.0199)	(0.0084)
		MC	3	0.0091	-0.0068	0.0067	-0.1365	-0.0255	-0.2154	-0.0213	0.0736
				(0.0188)	(0.0232)	(0.0056)	(0.0324)	(0.0575)	(0.0594)	(0.0111)	(0.0143)
Bovini											
Anoa depressicornis	Forest	MT	6	0.0387	-0.1147	-0.0563	-0.0767	0.0781	0.0282	0.025	-0.0182
				(0.017)	(0.0164)	(0.0196)	(0.0235)	(0.0258)	(0.0134)	(0.0095)	(0.0118)
		MC	6	0.0588	-0.0262	0.079	-0.1365	0.0992	-0.1778	0.0317	-0.0412
				(0.0164)	(0.0148)	(0.0207)	(0.0184)	(0.0202)	(0.0321)	(0.0108)	(0.0263)
Anoa mindorensis	Forest	MT	2	0.0836	-0.1324	-0.0333	-0.0989	0.1343	0.0313	0.0478	-0.0379
				(0.0096)	(0.0031)	(0.0136)	(0.0079)	(0.0165)	(0.0071)	(0.0015)	(0.0108)
		MC	2	0.1031	-0.0312	0.0831	-0.1674	0.1347	-0.1676	0.0517	-0.0234
				(0.0019)	(0.0075)	(0.0039)	(0.0003)	(0.0286)	(0.0216)	(0.0164)	(0.0238)
Bison bison athabaskae	Light cover	MT	5	-0.0113	-0.1186	-0.1142	-0.0764	0.0107	-0.019	0.0125	-0.0114

				(0.0119)	(0.0261)	(0.0208)	(0.0237)	(0.0112)	(0.011)	(0.0095)	(0.0224)
		MC	5	0.0213	-0.0406	0.0327	-0.1827	0.0326	-0.2193	0.011	-0.0398
				(0.0204)	(0.0202)	(0.0233)	(0.0241)	(0.0079)	(0.0151)	(0.0093)	(0.0175)
Bison bison bison	Plains	MT	6	-0.0233	-0.0994	-0.0958	-0.0486	0.0244	-0.0122	0.014	0.0007
				(0.0782)	(0.0238)	(0.0217)	(0.0155)	(0.0121)	(0.0118)	(0.0125)	(0.014)
		MC	5	0.0246	-0.029	0.0547	-0.1634	0.0404	-0.2098	0.0115	-0.0277
				(0.0079)	(0.0114)	(0.0213)	(0.0216)	(0.0222)	(0.0148)	(0.0144)	(0.0214)
Bos gaurus	Heavy cover	MT	5	0.0387	-0.0713	-0.079	-0.0241	0.0593	0.0237	0.0064	0.0045
				(0.0139)	(0.0073)	(0.0147)	(0.008)	(0.0102)	(0.0129)	(0.0052)	(0.0177)
		MC	5	0.0425	0.0072	0.0555	-0.0999	0.0367	-0.159	0.0125	0.0179
				(0.0091)	(0.0177)	(0.0208)	(0.0208)	(0.0117)	(0.0147)	(0.0063)	(0.0164)
Bos grunniens	Mountain	MT	4	0.0166	-0.1394	-0.0797	-0.0811	0.0536	-0.0001	0.036	-0.011
				(0.0145)	(0.0138)	(0.0094)	(0.0294)	(0.0796)	(0.0087)	(0.0043)	(0.0237)
		MC	4	0.0599	-0.0862	0.0951	-0.1693	0.1024	-0.2032	0.0465	-0.0181
				(0.0204)	(0.0206)	(0.023)	(0.0308)	(0.0266)	(0.0243)	(0.0098)	(0.0162)
Bos sauveli	Heavy cover	MT	2	-0.0197	-0.0762	-0.1132	0.0017	0.0208	0.0139	0.0009	0.015
				(0.0003)	(0.0166)	(0.0134)	(0.0128)	(0.0018)	(0.0226)	(0.0089)	(0.026)
		MC	2	-0.018	0.0546	0.0153	-0.1103	-0.0155	-0.183	-0.004	0.0096
				(0.0215)	(0.1214)	(0.031)	(0.0096)	(0.016)	(0.0187)	(0.0213)	(0.0109)
Bubalis bubalis	Heavy cover	MT	1	-0.0339	-0.1374	-0.1332	-0.1157	0.0321	-0.0154	0.0434	0.0077
		MC	1	-0.0118	-0.0699	0.0215	-0.184	0.0655	-0.2425	0.0457	-0.0406
Syncerus caffer caffer	Light cover	MT	3	0.0427	-0.1293	-0.0624	-0.0688	0.0807	0.0272	0.0202	-0.0001
				(0.0164)	(0.018)	(0.0032)	(0.0135)	(0.0055)	(0.0185)	(0.0077)	(0.012)
		MC	3	0.0874	-0.0236	0.0869	-0.1209	0.1226	-0.1405	0.0353	-0.0154
				(0.009)	(0.0175)	(0.011)	(0.0269)	(0.0244)	(0.0189)	(0.0125)	(0.0232)
Syncerus caffer nanus	Heavy cover	MT	3	0.0355	-0.1465	-0.073	-0.0969	0.0831	0.0204	0.0165	0.0033
				(0.0027)	(0.02)	(0.0204)	(0.0244)	(0.0051)	(0.0158)	(0.0051)	(0.0233)

		MC	3	0.0527	-0.0415	0.0672	-0.1623	0.0951	-0.1792	0.0207	-0.0249
				(0.0158)	(0.0197)	(0.0163)	(0.0132)	(0.0029)	(0.0156)	(0.0063)	(0.0182)
Tragelaphini											
Tragelaphus angasi	Heavy cover	MT	1	0.0161	-0.0921	-0.1239	-0.035	-0.0021	0.0078	-0.0404	0.01
		MC	1	-0.0461	-0.0077	-0.0586	-0.16	-0.086	-0.1783	-0.0408	0.0526
Tragelaphus derbianus	Light cover	MT	1	0.0175	-0.0857	-0.0799	-0.0296	-0.0282	0.0003	-0.0123	0.013
		MC	1	0.0007	0.0223	0.0241	-0.1061	-0.0191	-0.1812	-0.0111	0.0125
Tragelaphus eurycerus	Forest	MT	9	0.0356	-0.0961	-0.0785	-0.0464	0.0484	0.0412	-0.005	0.0391
				(0.0192)	(0.0128)	(0.0172)	(0.0165)	(0.0276)	(0.0134)	(0.0121)	(0.006)
		MC	9	0.022	0.0032	0.0187	-0.1089	0.0387	-0.143	0.0033	0.0563
				(0.0167)	(0.0159)	(0.0168)	(0.0381)	(0.0185)	(0.0251)	(0.0066)	(0.0099)
Tragelaphus imberbis	Heavy cover	MT	5	-0.0261	-0.0435	-0.1309	0.004	-0.0439	0.0286	-0.0231	0.0261
				(0.0176)	(0.0095)	(0.0199)	(0.0088)	(0.0159)	(0.008)	(0.0177)	(0.0119)
		MC	5	-0.0281	0.0505	-0.0362	-0.0678	-0.0672	-0.1496	-0.04	0.0489
				(0.0079)	(0.015)	(0.0158)	(0.0094)	(0.004)	(0.0111)	(0.0154)	(0.0106)
Tragelaphus oryx	Light cover	MT	6	0.0104	-0.1046	-0.0863	-0.0548	-0.0098	-0.0126	-0.0158	-0.0081
				(0.0177)	(0.0201)	(0.0274)	(0.0226)	(0.0449)	(0.015)	(0.018)	(0.0283)
		MC	6	0.0055	0.0079	0.0298	-0.1247	-0.0249	-0.1857	-0.0094	0.0092
				(0.0325)	(0.0131)	(0.0309)	(0.0094)	(0.0408)	(0.019)	(0.0167)	(0.023)
Tragelaphus scriptus	Forest	MT	14	0.0182	-0.0541	-0.0753	0.0068	0.0076	0.0304	-0.0134	0.0242
				(0.0238)	(0.0171)	(0.028)	(0.021)	(0.0231)	(0.0168)	(0.0157)	(0.0175)
		MC	15	0.008	0.0406	0.0134	-0.0815	-0.0171	-0.1428	-0.0213	0.0453
				(0.0288)	(0.0228)	(0.0161)	(0.0143)	(0.026)	(0.0187)	(0.0156)	(0.0195)
Tragelaphus spekei	Heavy cover	MT	6	0.0278	-0.1016	-0.0872	-0.0646	0.0423	0.0389	0.0068	0.0423
				(0.0232)	(0.0136)	(0.0186)	(0.0223)	(0.0254)	(0.0116)	(0.018)	(0.0206)

		MC	6	0.0125	0.0039	0.0091	-0.1386	0.032	-0.1263	0.007	0.0578
				(0.0201)	(0.0157)	(0.0172)	(0.0205)	(0.0127)	(0.0127)	(0.009)	(0.0123)
Tragelaphus strepsiceros	Heavy cover	MT	7	0.0019	-0.0735	-0.1145	-0.0176	-0.0311	0.0014	-0.0348	0.0258
				(0.0089)	(0.0186)	(0.0092)	(0.0236)	(0.0262)	(0.0184)	(0.0161)	(0.0086)
		MC	6	-0.02	0.0308	-0.0163	-0.0982	-0.0543	-0.1659	-0.0337	0.0616
				(0.0103)	(0.0184)	(0.0123)	(0.0244)	(0.0165)	(0.0335)	(0.0084)	(0.0153)
Caprinae											
Caprini											
Ammotragus lervia	Mountain	MT	4	0.0498	-0.1331	-0.0669	-0.0778	0.0482	-0.0132	0.0578	-0.0169
				(0.0342)	(0.0138)	(0.0299)	(0.0237)	(0.0278)	(0.0243)	(0.0089)	(0.0302)
		MC	4	0.0243	-0.0168	0.0168	-0.1373	0.0259	-0.1874	0.0544	-0.0246
				(0.0148)	(0.0216)	(0.0256)	(0.0425)	(0.018)	(0.0369)	(0.0135)	(0.0245)
Ovis ammon	Mountain	MT	5	0.0034	-0.1137	-0.1322	-0.0553	-0.0298	-0.0572	0.0108	-0.0614
				(0.0138)	(0.017)	(0.0175)	(0.0387)	(0.0249)	(0.0151)	(0.0103)	(0.0268)
		MC	5	-0.0103	-0.0062	-0.0133	-0.1022	-0.0344	-0.2061	0.0112	-0.0352
				(0.0205)	(0.0248)	(0.0254)	(0.0231)	(0.037)	(0.0145)	(0.0025)	(0.0288)
Pantholopini											
Pantholops hodgsoni	Plains	MT	1	-0.0522	-0.0918	-0.1658	-0.0473	-0.0853	-0.063	-0.0275	-0.0801
		MC	1	-0.0729	-0.0345	-0.0757	-0.1272	-0.0701	-0.2962	-0.0227	-0.0366
Rupicaprini											
Budorcas taxicolor	Mountain	MT	1	0.1018	-0.1788	-0.0446	-0.1511	0.1518	0.0217	0.042	-0.0356
		MC	1	0.1291	-0.0447	0.0692	-0.1998	0.1672	-0.146	0.0414	-0.035
Myotragus balearicus	Mountain	MT	1	0.2173	-0.0893	0.0797	-0.0568	0.2197	0.0547	0.0263	-0.0379

		MC	1	0.1988	0.0309	0.1899	-0.0915	0.2019	-0.1167	0.0592	-0.0059
Naemorhedus crispus	Mountain	MT	1	0.0225	-0.1661	-0.1042	-0.1377	0.034	-0.0901	0.0718	-0.073
		MC	1	0.0466	-0.062	0.0524	-0.1997	0.0828	-0.2274	0.0646	-0.0425
Naemorhedus goral	Mountain	MT	7	0.0201	-0.1355	-0.0941	-0.1046	0.0294	-0.022	0.0378	-0.0498
				(0.0301)	(0.0065)	(0.0235)	(0.0081)	(0.0301)	(0.0184)	(0.0134)	(0.0275)
		MC	7	0.0494	-0.0274	0.0491	-0.1625	0.0663	-0.1974	0.0363	-0.0414
				(0.0232)	(0.018)	(0.0196)	(0.0163)	(0.025)	(0.0235)	(0.008)	(0.0236)
Naemorhedus sumatraensis	Mountain	MT	5	0.0412	-0.1535	-0.0936	-0.1286	0.0318	-0.0353	0.0307	-0.0231
				(0.0109)	(0.0056)	(0.0152)	(0.0123)	(0.0249)	(0.0245)	(0.0112)	(0.0218)
		MC	5	0.0503	-0.0054	0.0277	-0.1754	0.0501	-0.1858	0.0338	-0.0125
				(0.0108)	(0.0684)	(0.0322)	(0.0118)	(0.0203)	(0.0229)	(0.01)	(0.0106)
Naemorhedus swinhoei	Mountain	MT	1	0.0946	-0.1489	-0.0242	-0.1259	0.1232	-0.0385	0.0574	-0.0881
		MC	1	0.1098	-0.0371	0.0972	-0.1635	0.1495	-0.1904	0.0665	-0.0559
Oreamnos americanus	Mountain	MT	3	0.1	-0.1734	-0.0704	-0.1266	0.1818	0.0055	0.0716	-0.032
				(0.0161)	(0.0087)	(0.0078)	(0.0113)	(0.0107)	(0.0141)	(0.0049)	(0.0046)
		MC	3	0.1277	-0.0757	0.0634	-0.2311	0.1781	-0.1409	0.0839	-0.0246
				(0.0102)	(0.0175)	(0.0133)	(0.0112)	(0.0141)	(0.0098)	(0.005)	(0.01)
Rupicapra rupicapra	Mountain	MT	1	0.0222	-0.1476	-0.1322	-0.056	0.0363	-0.0562	0.0459	-0.086
		MC	1	0.0213	-0.0393	0.0227	-0.1562	0.0454	-0.2089	0.0548	-0.0464
Cephalophinae											
Cephalophini											
Cephalophus	Forest	MT	5	0.0549	-0.0931	-0.0503	-0.0466	0.0881	0.0501	0.0079	0.0151

dorsalis				(0.0089)	(0.0065)	(0.016)	(0.0184)	(0.0212)	(0.0125)	(0.0078)	(0.0125)
		MC	5	0.0525	0.0026	0.0676	-0.121	0.0828	-0.1664	0.0178	-0.0079
				(0.0121)	(0.0096)	(0.0188)	(0.009)	(0.0065)	(0.0188)	(0.0114)	(0.0127)
Cephalophus leucogaster	Forest	MT	5	0.0175	-0.0874	-0.0878	-0.0301	0.0231	0.0222	-0.0054	-0.0087
				(0.0078)	(0.0183)	(0.0152)	(0.021)	(0.0203)	(0.0191)	(0.0094)	(0.0117)
		MC	5	0.0104	-0.001	0.0253	-0.1094	0.0151	-0.1917	0.0013	-0.0141
				(0.0212)	(0.0109)	(0.0143)	(0.0142)	(0.0135)	(0.0214)	(0.0091)	(0.0164)
Cephalophus sylvicultor	Forest	MT	7	0.0382	-0.1028	-0.0583	-0.0589	0.0493	0.0165	0.0171	0.0042
				(0.0148)	(0.0071)	(0.0173)	(0.0167)	(0.0254)	(0.0147)	(0.0076)	(0.0222)
		MC	7	0.0269	-0.0005	0.017	-0.1303	0.043	-0.1785	0.0208	-0.0089
				(0.0191)	(0.0081)	(0.0159)	(0.0102)	(0.031)	(0.0187)	(0.0052)	(0.022)
Cephalophus weynsi	Forest	MT	1	0.0344	-0.0925	-0.0862	-0.038	0.0689	0.0289	0.0094	0.0224
		MC	1	0.0244	-0.0235	0.0177	-0.1272	0.0613	-0.1869	0.0005	0.0127
Philantomba monticola	Forest	MT	1	0.072	-0.094	-0.0562	-0.0335	0.1102	0.0086	-0.0116	-0.0235
		MC	1	0.0472	-0.0367	0.0547	-0.1361	0.1131	-0.1923	-0.0064	-0.0212
Sylvicapra grimmia	Light cover	MT	7	0.019	-0.0931	-0.1032	-0.0286	0.0034	0.0121	-0.027	0.0054
				(0.0171)	(0.01)	(0.0111)	(0.0208)	(0.0248)	(0.0107)	(0.0185)	(0.0133)
		MC	9	0.0153	-0.007	0.0147	-0.1062	0.0109	-0.2049	-0.0201	-0.0125
				(0.0221)	(0.02)	(0.0154)	(0.0176)	(0.0391)	(0.0082)	(0.0235)	(0.02)
Hippotraginae											
Hippotragini											
Addax nasomaculatus	Plains	MT	4	-0.0336	-0.0769	-0.1412	-0.0209	-0.0301	-0.0159	0.0276	-0.0212
				(0.0076)	(0.0091)	(0.0163)	(0.0159)	(0.0112)	(0.0045)	(0.0052)	(0.0107)
		MC	4	-0.0399	-0.0047	-0.0401	-0.1289	-0.0031	-0.2035	0.0169	-0.0021

				(0.0104)	(0.0026)	(0.0229)	(0.0077)	(0.0032)	(0.0234)	(0.0079)	(0.0059)
Hippotragus equinus	Light cover	MT	5	-0.016	-0.1151	-0.1275	-0.0614	-0.0292	-0.0286	-0.0133	-0.0005
				(0.0091)	(0.0106)	(0.0107)	(0.0157)	(0.0225)	(0.0253)	(0.0092)	(0.0102)
		MC	5	-0.0276	-0.0065	-0.0291	-0.1192	-0.0196	-0.1967	-0.0195	-0.0045
				(0.0156)	(0.0192)	(0.0138)	(0.0266)	(0.024)	(0.0162)	(0.0117)	(0.0188)
Hippotragus niger	Light cover	MT	6	-0.0039	-0.103	-0.1101	-0.0351	-0.0244	-0.0057	-0.0034	0.0105
				(0.0247)	(0.0144)	(0.0167)	(0.0092)	(0.0285)	(0.0104)	(0.0136)	(0.0081)
		MC	6	-0.0155	-0.0084	-0.0284	-0.1194	-0.0188	-0.1932	-0.0118	-0.0029
				(0.0137)	(0.0072)	(0.0056)	(0.0153)	(0.0261)	(0.0088)	(0.015)	(0.0087)
Oryx beisa	Plains	MT	2	-0.0362	-0.0963	-0.1589	-0.0414	-0.0106	-0.023	0.005	-0.0233
				(0.0235)	(0.0308)	(0.0025)	(0.0192)	(0.0326)	(0.0002)	(0.0194)	(0.0019)
		MC	2	-0.0371	0.0045	-0.0266	-0.1218	-0.0313	-0.2039	-0.0056	-0.0384
				(0.0237)	(0.0145)	(0.0214)	(0.0049)	(0.0197)	(0.0144)	(0.0102)	(0.0258)
Oryx dammah	Plains	MT	2	-0.0529	-0.0853	-0.1578	-0.0279	-0.0434	0.005	0.0004	0.0246
				(0.0056)	(0.0109)	(0.0018)	(0.0002)	(0.0032)	(0.0093)	(0.0012)	(0.0043)
		MC	2	-0.0568	-0.0057	-0.0666	-0.1065	-0.0245	-0.1679	0.0081	0.0219
				(0.0007)	(0.0083)	(0.0009)	(0.0266)	(0.0056)	(0.0148)	(0.0018)	(0.0197)
Oryx gazella	Plains	MT	2	-0.0053	-0.1012	-0.1332	-0.0255	0.0123	-0.0025	0.0041	-0.0222
				(0.0028)	(0.0104)	(0.0019)	(0.0113)	(0.0279)	(0.0067)	(0.0113)	(0.0111)
		MC	2	-0.0103	-0.0157	-0.0204	-0.1208	0.0051	-0.206	0.0104	-0.0084
				(0.0119)	(0.0147)	(0.0097)	(0.0078)	(0.0083)	(0.0145)	(0.0033)	(0.0019)
Oryx leucoryx	Plains	MT	1	-0.045	-0.1412	-0.1344	-0.0696	-0.13	-0.0433	-0.0028	-0.0235
		MC	1	-0.0843	-0.0242	-0.0648	-0.1365	-0.1283	-0.2079	0.0034	-0.0393
Reduncinae											
Reduncini											
Kobus ellipsiprymnus	Heavy cover	MT	7	0.0015	-0.0914	-0.1093	-0.044	0.0111	0.0131	0.0066	0.0183
				(0.0197)	(0.0175)	(0.0152)	(0.0173)	(0.0218)	(0.0172)	(0.0034)	(0.0158)
		MC	8	-0.0146	0.0287	-0.0105	-0.1038	-0.0045	-0.1689	-0.0034	0.0029

				(0.0164)	(0.0237)	(0.0171)	(0.0286)	(0.0215)	(0.0263)	(0.008)	(0.0286)
Kobus kob	Light cover	MT	9	-0.0049	-0.0779	-0.1447	-0.021	0.0002	0.0131	0.0056	0.0188
				(0.0133)	(0.0108)	(0.0152)	(0.0113)	(0.0233)	(0.0257)	(0.0112)	(0.0117)
		MC	9	-0.0151	0.0381	-0.0272	-0.0909	-0.0177	-0.1805	0.0033	-0.0054
				(0.0203)	(0.016)	(0.017)	(0.0173)	(0.0273)	(0.0264)	(0.0108)	(0.0205)
Kobus leche	Light cover	MT	1	-0.0505	-0.1071	-0.16	-0.0571	-0.0536	0.0042	0.0017	0.0471
		MC	1	-0.0403	-0.009	-0.0163	-0.137	-0.0514	-0.2052	-0.0202	0.037
Kobus megaceros	Heavy cover	MT	6	-0.0041	-0.0885	-0.127	-0.0467	0.0126	0.0165	0.0029	0.0337
				(0.0139)	(0.0191)	(0.0216)	(0.0182)	(0.0232)	(0.015)	(0.0128)	(0.0261)
		MC	6	-0.0241	0.0277	-0.0285	-0.0949	-0.0264	-0.1678	-0.0042	0.0116
				(0.013)	(0.0193)	(0.0168)	(0.0176)	(0.027)	(0.0174)	(0.0128)	(0.0181)
Redunca arundinum	Light cover	MT	5	0.0004	-0.0698	-0.1369	-0.0172	-0.0371	0.0195	-0.0347	0.0692
				(0.0162)	(0.0102)	(0.0134)	(0.0109)	(0.038)	(0.0085)	(0.0234)	(0.0586)
		MC	5	-0.0273	0.0356	-0.0341	-0.0983	-0.0605	-0.1664	-0.031	0.0329
				(0.0127)	(0.0072)	(0.0206)	(0.0052)	(0.0316)	(0.0206)	(0.0058)	(0.0148)
Redunca fulvorufula	Light cover	MT	7	0.0068	-0.0852	-0.1154	-0.0413	-0.0096	-0.0101	-0.0024	0.0273
				(0.0192)	(0.0105)	(0.0119)	(0.0109)	(0.0158)	(0.0186)	(0.0073)	(0.0287)
		MC	7	-0.0096	0.0282	-0.0032	-0.1037	-0.0368	-0.1728	-0.004	0.0267
				(0.0142)	(0.0076)	(0.0094)	(0.0067)	(0.0265)	(0.0119)	(0.01)	(0.0204)
Redunca redunca	Light cover	MT	5	0.0072	-0.0664	-0.1147	-0.0065	-0.0284	0.0237	-0.0148	0.0363
				(0.0291)	(0.0103)	(0.0195)	(0.0198)	(0.031)	(0.0132)	(0.0108)	(0.0115)
		MC	5	-0.0027	0.0429	-0.0011	-0.0849	-0.0464	-0.1502	-0.0271	0.0439
				(0.0114)	(0.0124)	(0.0196)	(0.0133)	(0.0208)	(0.0125)	(0.0064)	(0.0203)

Table A4: Summary by species of anterior-posterior distal epiphyseal variables based on analysis of complete metapodials.

Species	Habitat	Elem.	*N*	EMAP	MVAP	IMAP	ELAP	LVAP	ILAP	DEAP
Antilocapridae										
Antilocaprinae										
Antilocaprini										
Antilocapra americana	Plains	MT	11	0.0223	0.015	0.0213	0.0291	0.0175	0.0166	-0.1168
				(0.009)	(0.0094)	(0.0092)	(0.0105)	(0.0102)	(0.0094)	(0.0151)
		MC	6	0.014	0.0153	0.0199	0.0246	0.0174	0.0189	-0.1091
				(0.0081)	(0.0098)	(0.0057)	(0.015)	(0.0089)	(0.0066)	(0.0096)
Bovidae										
Aepycerotinae										
Aepycerotini										
Aepyceros melampus	Light cover	MT	11	0.0458	0.0141	0.0239	0.0504	0.0133	0.0179	-0.1173
				(0.0208)	(0.0095)	(0.0129)	(0.0214)	(0.0091)	(0.0109)	(0.0153)
		MC	11	0.0375	0.0178	0.0244	0.0484	0.0236	0.0255	-0.1097
				(0.02)	(0.0118)	(0.015)	(0.0196)	(0.0091)	(0.0121)	(0.0114)
Alcelaphinae										
Alcelaphini										
Alcelaphus buselaphus	Plains	MT	9	0.019	0.0031	0.0071	0.0192	0.0013	-0.0023	-0.1096
				(0.0108)	(0.0082)	(0.0095)	(0.0091)	(0.0076)	(0.0082)	(0.0176)
		MC	9	0.0329	0.0151	0.0174	0.0301	0.008	0.0114	-0.1004
				(0.0073)	(0.009)	(0.0065)	(0.0066)	(0.0169)	(0.006)	(0.0178)
Alcelaphus lichtensteini	Plains	MT	1	0.0151	-0.002	0.0045	0.0242	-0.001	-0.0084	-0.1848
		MC	1	0.0327	0.0091	0.0108	0.0311	0.0107	0.0185	-0.1316
Beatragus hunteri	Plains	MT	3	0.0106	0.005	0.0092	0.0196	-0.0023	0.0031	-0.1238
				(0.0067)	(0.0012)	(0.0006)	(0.0035)	(0.0015)	(0.0011)	(0.0373)

		MC	3	0.0392	0.0093	0.017	0.0335	0.0043	0.0192	-0.0854
				(0.0027)	(0.0028)	(0.0043)	(0.0083)	(0.003)	(0.0074)	(0.0304)
Connochaetes gnou	Plains	MT	4	0.0006	0.0011	0.0064	-0.0096	-0.006	-0.0015	-0.1347
				(0.0062)	(0.0043)	(0.0046)	(0.0031)	(0.0065)	(0.0081)	(0.0297)
		MC	4	0.004	0.0086	-0.0024	-0.0023	0.0046	0.0015	-0.1323
				(0.0076)	(0.0067)	(0.0038)	(0.0024)	(0.0077)	(0.0063)	(0.0158)
Connochaetes taurinus	Plains	MT	6	-0.0121	-0.0038	-0.0091	-0.0235	-0.0069	-0.0106	-0.1386
				(0.0104)	(0.0031)	(0.0113)	(0.0181)	(0.0045)	(0.0083)	(0.037)
		MC	6	-0.0008	-0.0037	-0.0085	0.0029	-0.0046	-0.0089	-0.1284
				(0.0129)	(0.004)	(0.0125)	(0.0197)	(0.0054)	(0.0096)	(0.0195)
Damaliscus dorcas	Plains	MT	5	0.0268	0.0034	0.0099	0.0217	0.0008	0.0035	-0.1153
				(0.011)	(0.0036)	(0.0041)	(0.0135)	(0.005)	(0.0084)	(0.0268)
		MC	5	0.0417	0.0112	0.0223	0.0398	0.009	0.0209	-0.0966
				(0.0104)	(0.0089)	(0.01)	(0.0134)	(0.0099)	(0.0111)	(0.0157)
Damaliscus lunatus	Plains	MT	7	0.0116	0.0022	-0.0011	0.008	-0.0015	-0.0022	-0.1148
				(0.0164)	(0.0101)	(0.0051)	(0.0082)	(0.0081)	(0.0068)	(0.0266)
		MC	7	0.0361	0.0118	0.0091	0.0304	0.006	0.012	-0.104
				(0.0095)	(0.0078)	(0.0092)	(0.0115)	(0.009)	(0.0084)	(0.0111)
Antilopinae										
Antilopini										
Antidorcas marsupialis	Plains	MT	5	0.0198	0.0126	0.0133	0.0257	0.0091	0.0087	-0.1215
				(0.0119)	(0.0088)	(0.0144)	(0.0144)	(0.0087)	(0.0101)	(0.0304)
		MC	5	0.0422	0.0216	0.0228	0.0397	0.0177	0.0203	-0.1241
				(0.0127)	(0.009)	(0.0167)	(0.0121)	(0.0073)	(0.0116)	(0.0127)
Antilope cervicapra	Plains	MT	3	0.0103	0.0131	0.0069	0.0027	0.0033	-0.0003	-0.1381
				(0.0133)	(0.0067)	(0.0114)	(0.0029)	(0.0043)	(0.0117)	(0.0397)
		MC	3	0.0181	0.0167	0.0166	0.0203	0.0109	0.0134	-0.1465
				(0.0109)	(0.0107)	(0.0148)	(0.0147)	(0.01)	(0.0156)	(0.0049)
Eudorcas rufifrons	Plains	MT	1	0.0132	0.0155	0.014	0.0215	0.0145	0.0109	-0.1062

		MC	1	0.0405	0.0298	0.0269	0.0389	0.0248	0.0242	-0.1271
Eudorcas thomsoni	Plains	MT	6	0.0028	0.0142	0.0035	0.0108	0.0113	0.0035	-0.1297
				(0.0124)	(0.0055)	(0.0067)	(0.011)	(0.0052)	(0.0068)	(0.0255)
		MC	6	0.0163	0.0213	0.0148	0.0192	0.0214	0.0179	-0.1175
				(0.0065)	(0.0072)	(0.0113)	(0.0096)	(0.0068)	(0.0123)	(0.0126)
Gazella gazella	Plains	MT	1	-0.004	0.0051	0.0025	-0.0075	0.0005	0.0038	-0.1054
		MC	1	0.0182	0.0166	0.016	0.0165	0.0151	0.02	-0.0977
Litocranius walleri	Light cover	MT	5	0.0242	0.0243	0.019	0.0304	0.0198	0.0088	-0.0732
				(0.0067)	(0.0063)	(0.0068)	(0.0116)	(0.0083)	(0.0089)	(0.0067)
		MC	5	0.0533	0.0338	0.0305	0.0519	0.0295	0.0283	-0.0861
				(0.0078)	(0.006)	(0.0097)	(0.0098)	(0.0074)	(0.0089)	(0.0259)
Nanger granti	Plains	MT	9	0.0207	0.0165	0.0146	0.0161	0.0152	0.0138	-0.0962
				(0.0068)	(0.0062)	(0.0049)	(0.0108)	(0.0057)	(0.0055)	(0.0128)
		MC	9	0.0401	0.0317	0.0297	0.0421	0.0336	0.0348	-0.0865
				(0.0098)	(0.0049)	(0.0074)	(0.0185)	(0.0075)	(0.0077)	(0.0157)
Nanger soemmerringi	Plains	MT	2	0.0135	0.0179	0.0072	0.0095	0.0128	0.0069	-0.1144
				(0.002)	(0.0023)	(0.0056)	(0.0051)	(0.0064)	(0.0027)	(0.0093)
		MC	2	0.0309	0.029	0.0272	0.0346	0.0307	0.0293	-0.1008
				(0.0084)	(0.0044)	(0.0016)	(0.0069)	(0.01)	(0.0067)	(0.0186)
Neotragini										
Madoqua guentheri	Heavy cover	MT	3	0.0093	0.0096	0.0056	-0.0076	0.0025	0.0035	-0.0847
				(0.0083)	(0.0144)	(0.0128)	(0.009)	(0.0096)	(0.0104)	(0.0108)
		MC	3	-0.0109	-0.0023	-0.0063	-0.0269	-0.0075	-0.0083	-0.1281
				(0.0206)	(0.0123)	(0.0059)	(0.0086)	(0.0094)	(0.0073)	(0.0158)
Madoqua kirki	Heavy cover	MT	6	-0.002	-0.0045	-0.0019	-0.0089	-0.0059	-0.0044	-0.1072
				(0.0054)	(0.0052)	(0.012)	(0.0133)	(0.0066)	(0.0095)	(0.0185)

		MC	6	-0.0172	-0.0122	-0.0099	-0.0277	-0.0156	-0.0127	-0.1293
				(0.0061)	(0.0078)	(0.0064)	(0.0077)	(0.0063)	(0.0099)	(0.0247)
Madoqua sp.	Heavy cover	MT	3	-0.0066	0.0076	0.0013	-0.0049	0.0093	-0.0015	-0.09
				(0.0101)	(0.0087)	(0.0058)	(0.0116)	(0.0091)	(0.0066)	(0.0218)
		MC	3	-0.0221	-0.0042	-0.0131	-0.0318	-0.005	-0.0144	-0.113
				(0.0147)	(0.0093)	(0.0049)	(0.0118)	(0.0082)	(0.0014)	(0.0126)
Neotragus batesi	Forest	MT	1	-0.0089	-0.005	-0.0127	-0.0464	-0.0085	-0.0104	-0.0734
		MC	1	-0.0296	-0.0061	-0.0363	-0.0704	-0.0194	-0.0358	-0.0933
Nesotragus moschatus	Forest	MT	1	0.0045	-0.0268	-0.0262	-0.0325	-0.0251	-0.0192	-0.0572
		MC	1	-0.0201	-0.0257	-0.0298	-0.0667	-0.0446	-0.0287	-0.0711
Oreotragus oreotragus	Mountain	MT	7	0.0053	0.0206	-0.0038	0.0228	0.0226	-0.0123	-0.1153
				(0.0191)	(0.01)	(0.0048)	(0.0199)	(0.0129)	(0.0126)	(0.0114)
		MC	7	-0.031	0.0047	-0.031	-0.0372	-0.0014	-0.0439	-0.1596
				(0.0136)	(0.0082)	(0.0108)	(0.0188)	(0.0099)	(0.0142)	(0.0212)
Ourebia ourebi	Light cover	MT	7	-0.01	0.0064	0.0064	-0.0033	0.0055	0.0041	-0.1144
				(0.0114)	(0.0054)	(0.0101)	(0.0194)	(0.0075)	(0.0108)	(0.0188)
		MC	7	0.0014	0.008	0.0134	-0.0002	0.0088	0.0135	-0.1058
				(0.0095)	(0.0077)	(0.0087)	(0.0125)	(0.0074)	(0.0083)	(0.0159)
Raphicerus campestris	Light cover	MT	5	-0.025	0.0053	0.0005	-0.0055	-0.0011	0.0017	-0.0285
				(0.0077)	(0.0046)	(0.0053)	(0.0096)	(0.0156)	(0.0087)	(0.0781)
		MC	5	-0.0194	-0.0077	-0.0021	-0.0099	-0.0034	-0.0004	-0.0963
				(0.0123)	(0.01)	(0.0142)	(0.0108)	(0.0083)	(0.0153)	(0.0171)
Raphicerus sharpei	Light cover	MT	1	-0.0216	-0.0055	-0.0046	-0.0139	-0.0034	0.0014	-0.0964
		MC	1	-0.02	-0.0075	-0.0103	-0.0111	-0.0103	-0.0104	-0.0971

Saigini										
Saiga tatarica	Plains	MT	3	-0.0115	0.0095	-0.0036	-0.0143	0.0014	-0.0058	-0.1515
				(0.0076)	(0.0011)	(0.003)	(0.0041)	(0.0013)	(0.0052)	(0.0239)
		MC	3	0.0098	0.0126	0.0009	-0.002	0.0056	-0.0046	-0.1118
				(0.0048)	(0.0014)	(0.0063)	(0.0053)	(0.0005)	(0.0052)	(0.0124)
Bovinae										
Boselaphini										
Boselaphus tragocamelus	Heavy cover	MT	5	0.02	0.0222	0.0247	0.0501	0.0324	0.0218	-0.0596
				(0.017)	(0.0147)	(0.0104)	(0.0254)	(0.0142)	(0.006)	(0.0409)
		MC	6	0.0337	0.0363	0.032	0.0504	0.0432	0.0343	-0.0446
				(0.0113)	(0.0149)	(0.013)	(0.01)	(0.0172)	(0.0112)	(0.0468)
Tetracerus quadricornis	Heavy cover	MT	4	0.0151	-0.0089	-0.0016	0.0092	-0.0077	0.0054	-0.156
				(0.0168)	(0.0156)	(0.013)	(0.0211)	(0.0169)	(0.0143)	(0.0201)
		MC	3	0.031	0.0216	0.02	0.0316	0.0174	0.018	-0.11
				(0.0086)	(0.0128)	(0.0098)	(0.009)	(0.0164)	(0.0083)	(0.0129)
Bovini										
Anoa depressicornis	Forest	MT	6	-0.0348	-0.034	-0.0229	-0.0397	-0.044	-0.0263	-0.1078
				(0.0099)	(0.0086)	(0.0129)	(0.0121)	(0.0098)	(0.0157)	(0.0173)
		MC	6	-0.0504	-0.0414	-0.0374	-0.0649	-0.0484	-0.0373	-0.1182
				(0.0073)	(0.0169)	(0.0147)	(0.0136)	(0.0097)	(0.0174)	(0.0229)
Anoa mindorensis	Forest	MT	2	-0.0253	-0.0379	-0.0333	-0.0593	-0.0548	-0.0346	-0.0946
				(0.0052)	(0.0074)	(0.0116)	(0.0144)	(0.0051)	(0.0003)	(0.0238)
		MC	2	-0.0504	-0.0425	-0.0384	-0.0783	-0.0622	-0.0428	-0.1027
				(0.0109)	(0.0123)	(0.0103)	(0.0033)	(0.0018)	(0.0003)	(0.0238)
Bison bison athabaskae	Light cover	MT	5	-0.0097	0.0037	-0.0026	-0.0161	-0.0038	0.0007	-0.0887
				(0.0085)	(0.0098)	(0.0107)	(0.0151)	(0.0122)	(0.0098)	(0.0213)
		MC	5	-0.0223	-0.0126	-0.0148	-0.0324	-0.0195	-0.0146	-0.1179
				(0.0055)	(0.0098)	(0.0073)	(0.0049)	(0.0105)	(0.0063)	(0.0123)
Bison bison bison	Plains	MT	6	-0.0068	-0.0027	-0.0031	-0.015	-0.0076	0	-0.0839
				(0.0143)	(0.0124)	(0.0126)	(0.0187)	(0.0161)	(0.0135)	(0.0177)

		MC	5	-0.0209	-0.0193	-0.0176	-0.0373	-0.029	-0.0175	-0.1311
				(0.009)	(0.0106)	(0.0126)	(0.0098)	(0.0088)	(0.0145)	(0.0073)
Bos gaurus	Heavy cover	MT	5	-0.0284	-0.0304	-0.0274	-0.0142	-0.0174	-0.0135	-0.1053
				(0.005)	(0.0069)	(0.0084)	(0.0104)	(0.0057)	(0.0078)	(0.0122)
		MC	5	-0.0327	-0.0318	-0.0199	-0.0331	-0.0282	-0.0229	-0.0929
				(0.0101)	(0.0109)	(0.0086)	(0.0047)	(0.008)	(0.0096)	(0.0138)
Bos grunniens	Mountain	MT	4	-0.0306	-0.0051	-0.0188	-0.0352	-0.0085	-0.011	-0.0997
				(0.0143)	(0.0082)	(0.0086)	(0.0085)	(0.0151)	(0.0087)	(0.0179)
		MC	4	-0.0345	-0.0188	-0.0366	-0.0718	-0.0296	-0.039	-0.114
				(0.0205)	(0.0123)	(0.0095)	(0.0225)	(0.0167)	(0.0107)	(0.0148)
Bos sauveli	Heavy cover	MT	2	-0.0027	-0.0162	-0.0069	0.0108	-0.0082	0.0043	-0.0777
				(0.0046)	(0.0006)	(0.0033)	(0.0067)	(0.0058)	(0.0023)	(0.0031)
		MC	2	-0.0281	-0.0282	-0.0205	-0.0243	-0.0234	-0.0146	-0.0903
				(0.0116)	(0.0055)	(0.0234)	(0.0099)	(0.004)	(0.0115)	(0.0116)
Bubalis bubalis	Heavy cover	MT	1	-0.0093	-0.0173	-0.0112	-0.0813	-0.0365	-0.0181	-0.0805
		MC	1	-0.0344	-0.0336	-0.0358	-0.0564	-0.0319	-0.0193	-0.1178
Syncerus caffer caffer	Light cover	MT	3	-0.0149	-0.0206	-0.0208	-0.0665	-0.02	-0.0138	-0.1248
				(0.0537)	(0.0025)	(0.005)	(0.0055)	(0.0058)	(0.0057)	(0.012)
		MC	3	-0.0513	-0.0377	-0.0451	-0.0714	-0.0347	-0.0358	-0.1346
				(0.0088)	(0.0024)	(0.0056)	(0.0146)	(0.0072)	(0.0055)	(0.0198)
Syncerus caffer nanus	Heavy cover	MT	3	-0.0261	-0.0046	-0.0226	-0.0555	-0.0131	-0.0164	-0.0908
				(0.0108)	(0.0035)	(0.0029)	(0.0112)	(0.0063)	(0.0054)	(0.0138)
		MC	3	-0.035	-0.023	-0.0349	-0.0465	-0.0196	-0.0274	-0.1143
				(0.0104)	(0.0129)	(0.0114)	(0.0103)	(0.0096)	(0.011)	(0.0032)
Tragelaphini										
Tragelaphus angasi	Heavy cover	MT	1	0.0554	0.0154	0.024	0.0572	0.016	0.0303	-0.0694

		MC	1	0.0757	0.0343	0.0437	0.1024	0.0423	0.0485	-0.0117
Tragelaphus derbianus	Light cover	MT	1	0.0101	0.0056	0.0161	0.0044	-0.002	0.0081	-0.0971
		MC	1	-0.0085	0.0026	0.0056	0.0037	-0.0024	0.0023	-0.0758
Tragelaphus eurycerus	Forest	MT	9	0.0038	-0.007	0.0068	0.0002	0.0011	0.0131	-0.1666
				(0.0122)	(0.0107)	(0.0148)	(0.0179)	(0.0146)	(0.0135)	(0.0636)
		MC	9	0.001	0.0014	0.0112	0.0078	0.0017	-0.0035	-0.1361
				(0.014)	(0.0126)	(0.0134)	(0.0143)	(0.0143)	(0.0226)	(0.0595)
Tragelaphus imberbis	Heavy cover	MT	5	0.0561	0.013	0.0287	0.0627	0.015	0.0261	-0.1159
				(0.0156)	(0.0108)	(0.0114)	(0.0168)	(0.0094)	(0.0114)	(0.0265)
		MC	5	0.0645	0.0248	0.0421	0.0712	0.0298	0.0388	-0.0821
				(0.0103)	(0.0085)	(0.0108)	(0.0094)	(0.0103)	(0.0136)	(0.0238)
Tragelaphus oryx	Light cover	MT	6	0.0066	-0.0005	0.0041	0.0093	0.0001	0.005	-0.083
				(0.0104)	(0.0128)	(0.0145)	(0.006)	(0.0103)	(0.0129)	(0.0167)
		MC	6	0.0076	-0.0024	0.0035	0.008	-0.0045	-0.0009	-0.0733
				(0.014)	(0.0112)	(0.0127)	(0.0121)	(0.01)	(0.0162)	(0.0141)
Tragelaphus scriptus	Forest	MT	14	0.0169	-0.0083	-0.0102	0.0119	-0.0036	0.009	-0.1176
				(0.0129)	(0.0128)	(0.0137)	(0.0133)	(0.0162)	(0.0163)	(0.0564)
		MC	15	0.0258	0.0029	0.0094	0.0278	0.0052	0.0113	-0.0828
				(0.0097)	(0.009)	(0.0106)	(0.0113)	(0.0098)	(0.0103)	(0.0429)
Tragelaphus spekei	Heavy cover	MT	6	0.029	-0.0153	0.0027	0.0416	-0.0074	0.0123	-0.1507
				(0.0064)	(0.0099)	(0.0102)	(0.0094)	(0.009)	(0.0089)	(0.0525)
		MC	6	0.0245	-0.005	0.0101	0.0377	0.0043	0.0135	-0.1206
				(0.0084)	(0.0056)	(0.0077)	(0.0087)	(0.0046)	(0.0053)	(0.0417)
Tragelaphus strepsiceros	Heavy cover	MT	7	0.0358	0.0093	0.0268	0.0525	0.018	0.0223	-0.1009
				(0.0113)	(0.0084)	(0.0151)	(0.0182)	(0.0113)	(0.0104)	(0.0404)

		MC	6	0.0446	0.0219	0.031	0.0515	0.0283	0.0308	-0.0649
				(0.0161)	(0.0064)	(0.0127)	(0.0176)	(0.0072)	(0.0154)	(0.04)
Caprinae										
Caprini										
Ammotragus lervia	Mountain	MT	4	-0.063	-0.0051	-0.016	-0.0502	-0.0032	-0.0212	-0.1045
				(0.0449)	(0.0172)	(0.0041)	(0.0126)	(0.0101)	(0.0075)	(0.0221)
		MC	4	-0.0609	-0.0176	-0.03	-0.0704	-0.0228	-0.0272	-0.109
				(0.0251)	(0.0207)	(0.0107)	(0.0104)	(0.0145)	(0.0075)	(0.0339)
Ovis ammon	Mountain	MT	5	-0.005	0.0242	0.0063	-0.0058	0.0158	-0.0065	-0.1221
				(0.0098)	(0.0091)	(0.011)	(0.0114)	(0.0098)	(0.0154)	(0.0197)
		MC	5	-0.0084	0.0134	-0.0015	-0.0089	0.0094	-0.0035	-0.1098
				(0.0072)	(0.0069)	(0.0123)	(0.0088)	(0.008)	(0.0095)	(0.0258)
Pantholopini										
Pantholops hodgsoni	Plains	MT	1	0.0232	0.0115	0.012	0.0139	0.0035	0.005	-0.1438
		MC	1	0.0488	0.0259	0.0135	0.0308	0.0183	0.0182	-0.1056
Rupicaprini										
Budorcas taxicolor	Mountain	MT	1	-0.0651	0.0068	-0.0099	-0.0632	0.0111	-0.0036	-0.1001
		MC	1	-0.0979	-0.0198	-0.0355	-0.1044	-0.0177	-0.047	-0.1357
Myotragus balearicus	Mountain	MT	1	-0.1005	-0.0914	-0.0632	-0.0791	-0.0801	-0.0653	-0.1615
		MC	1	-0.1181	-0.0918	-0.0666	-0.098	-0.0849	-0.0636	-0.1439
Naemorhedus crispus	Mountain	MT	1	-0.0798	0.002	-0.0115	-0.0788	-0.002	-0.0195	-0.1215
		MC	1	-0.0837	-0.0012	-0.0183	-0.0831	-0.0139	-0.0341	-0.1671
Naemorhedus goral	Mountain	MT	7	-0.0697	-0.0153	-0.0195	-0.0471	-0.013	-0.0178	-0.1333

				(0.0177)	(0.0087)	(0.0099)	(0.0191)	(0.01)	(0.0109)	(0.0152)
		MC	7	-0.0901	-0.0306	-0.0293	-0.1009	-0.031	-0.0358	-0.1582
				(0.0187)	(0.0068)	(0.0093)	(0.0187)	(0.0067)	(0.0043)	(0.0261)
Naemorhedus sumatraensis	Mountain	MT	5	-0.047	0.0086	0.0021	-0.0408	0.0085	-0.005	-0.1138
				(0.0137)	(0.0069)	(0.0061)	(0.0182)	(0.0066)	(0.0065)	(0.0147)
		MC	5	-0.073	-0.0063	-0.0166	-0.0674	-0.0028	-0.0272	-0.1184
				(0.0118)	(0.0117)	(0.0189)	(0.0131)	(0.0134)	(0.0192)	(0.0102)
Naemorhedus swinhoei	Mountain	MT	1	-0.087	-0.0314	-0.0606	-0.0906	-0.0303	-0.0458	-0.1769
		MC	1	-0.1096	-0.0519	-0.0656	-0.1204	-0.0347	-0.0647	-0.1359
Oreamnos americanus	Mountain	MT	3	-0.0812	-0.0143	-0.0304	-0.0597	-0.0134	-0.0463	-0.1351
				(0.014)	(0.0013)	(0.0057)	(0.0168)	(0.0007)	(0.0061)	(0.0046)
		MC	3	-0.1316	-0.0229	-0.0576	-0.1282	-0.0239	-0.0691	-0.1324
				(0.0028)	(0.0019)	(0.0109)	(0.0089)	(0.0077)	(0.0125)	(0.0046)
Rupicapra rupicapra	Mountain	MT	1	-0.0352	0.019	-0.0264	-0.0366	0.0133	-0.0302	-0.1459
		MC	1	-0.0623	0.0093	-0.0365	-0.0844	0.0069	-0.037	-0.1357
Cephalophinae										
Cephalophini										
Cephalophus dorsalis	Forest	MT	5	-0.0184	-0.0351	-0.0157	-0.036	-0.0276	-0.0038	-0.1306
				(0.0049)	(0.0079)	(0.0056)	(0.0031)	(0.0113)	(0.0079)	(0.0806)
		MC	5	-0.0251	-0.0403	-0.0185	-0.0262	-0.0393	-0.0219	-0.1366
				(0.0112)	(0.0083)	(0.0038)	(0.0154)	(0.0105)	(0.0026)	(0.0459)
Cephalophus leucogaster	Forest	MT	5	-0.0026	-0.027	-0.0009	-0.0127	-0.0186	0.0025	-0.0889
				(0.0094)	(0.0093)	(0.0114)	(0.0134)	(0.0125)	(0.0129)	(0.0199)
		MC	5	-0.0145	-0.0322	-0.0186	-0.0009	-0.0297	-0.0161	-0.0909
				(0.013)	(0.0059)	(0.0115)	(0.007)	(0.0048)	(0.0116)	(0.0205)
Cephalophus sylvicultor	Forest	MT	7	-0.0182	-0.0222	-0.0051	-0.0275	-0.0148	0.0042	-0.1479
				(0.0115)	(0.0075)	(0.0081)	(0.0096)	(0.0105)	(0.0104)	(0.0645)

		MC	7	-0.0207	-0.0268	-0.0089	-0.0088	-0.0216	-0.0086	-0.1436
				(0.0157)	(0.0076)	(0.0103)	(0.0185)	(0.0071)	(0.0092)	(0.0378)
Cephalophus weynsi	Forest	MT	1	-0.0306	-0.03	0.0157	0.0077	-0.0201	0.0046	-0.0667
		MC	1	-0.0127	-0.0281	-0.0104	-0.0178	-0.0158	-0.0079	-0.0788
Philantomba monticola	Forest	MT	1	-0.0016	-0.0317	-0.0086	-0.0632	-0.0304	-0.0007	-0.1008
		MC	1	-0.0098	-0.0202	0.0003	-0.027	-0.027	-0.0047	-0.0962
Sylvicapra grimmia	Light cover	MT	7	0.0141	-0.015	0.0059	0.0117	-0.0111	0.0136	-0.0889
				(0.0215)	(0.0174)	(0.014)	(0.0208)	(0.0168)	(0.0127)	(0.0221)
		MC	9	0.0099	-0.0048	-0.0035	0.0134	-0.0104	-0.0007	-0.0912
				(0.0175)	(0.0394)	(0.0142)	(0.0195)	(0.0164)	(0.0139)	(0.0172)
Hippotraginae										
Hippotragini										
Addax nasomaculatus	Plains	MT	4	-0.0382	-0.0144	-0.0187	-0.0376	-0.0209	-0.0294	-0.1012
				(0.0131)	(0.0118)	(0.0044)	(0.0082)	(0.0092)	(0.0017)	(0.0089)
		MC	4	-0.0115	-0.0078	-0.0106	-0.029	-0.0126	-0.014	-0.0865
				(0.0112)	(0.0112)	(0.0072)	(0.0121)	(0.0104)	(0.0027)	(0.0223)
Hippotragus equinus	Light cover	MT	5	-0.007	0.0087	0.0125	0.0109	0.01	0.0086	-0.1288
				(0.0121)	(0.007)	(0.0063)	(0.0108)	(0.0076)	(0.0052)	(0.0253)
		MC	5	0.0094	0.0167	0.0144	0.0126	0.0145	0.0153	-0.1056
				(0.0164)	(0.0115)	(0.0115)	(0.0163)	(0.0093)	(0.0106)	(0.0207)
Hippotragus niger	Light cover	MT	6	0.0089	0.0049	0.0058	0.0077	0.0065	0.0032	-0.1613
				(0.0164)	(0.0072)	(0.0074)	(0.0188)	(0.0082)	(0.0059)	(0.0427)
		MC	6	0.0033	0.0069	-0.0022	0.0063	0.0045	-0.0022	-0.1396
				(0.0072)	(0.0107)	(0.0114)	(0.0095)	(0.0108)	(0.0095)	(0.0364)
Oryx beisa	Plains	MT	2	-0.0084	-0.0047	-0.0183	-0.0155	-0.002	-0.0115	-0.1045
				(0.0073)	(0.0131)	(0.0064)	(0.0021)	(0.0153)	(0.0101)	(0.0062)

		MC	2	-0.0037	-0.0008	-0.0104	-0.0083	0.0009	-0.0072	-0.1166
				(0.007)	(0.0155)	(0.0099)	(0.0043)	(0.0156)	(0.0087)	(0.0117)
Oryx dammah	Plains	MT	2	0.0039	0.0004	0.0053	0.0093	0.0038	0.0031	-0.0815
				(0.0014)	(0.0096)	(0.0144)	(0.0046)	(0.0086)	(0.0141)	(0.0115)
		MC	2	0.012	0.0018	-0.0039	0.0139	0.0028	0.0014	-0.0854
				(0.0028)	(0.003)	(0.0019)	(0.0013)	(0.0056)	(0.0007)	(0.0074)
Oryx gazella	Plains	MT	2	-0.0157	0.0037	-0.0007	-0.0151	0.0022	-0.0121	-0.0972
				(0.0116)	(0.0007)	(0.0125)	(0.0068)	(0.0031)	(0.0022)	(0.0034)
		MC	2	0.0042	0.0066	-0.0091	-0.0143	0.0019	-0.0132	-0.0842
				(0.0057)	(0.0056)	(0.0001)	(0.0055)	(0.0003)	(0.0018)	(0.0099)
Oryx leucoryx	Plains	MT	1	-0.0081	0.0067	-0.006	-0.0163	0.0081	0.0047	-0.1166
		MC	1	0.0047	0.0137	0.0077	-0.0018	0.0144	0.0067	-0.1402
Reduncinae										
Reduncini										
Kobus ellipsiprymnus	Heavy cover	MT	7	-0.0199	0.0057	-0.0116	-0.0224	-0.0033	-0.0112	-0.131
				(0.0169)	(0.0166)	(0.0163)	(0.0162)	(0.0189)	(0.015)	(0.0613)
		MC	8	-0.0154	-0.0008	-0.0106	-0.0109	0.0047	-0.0031	-0.1258
				(0.0173)	(0.0121)	(0.0162)	(0.0227)	(0.014)	(0.0134)	(0.0395)
Kobus kob	Light cover	MT	9	-0.0019	-0.0053	-0.0162	-0.0105	-0.0068	-0.0179	-0.1335
				(0.01)	(0.0067)	(0.0045)	(0.006)	(0.0037)	(0.0072)	(0.0638)
		MC	9	-0.0092	-0.0101	-0.0053	-0.0056	-0.0088	-0.0033	-0.1423
				(0.0104)	(0.0074)	(0.0108)	(0.016)	(0.0085)	(0.0096)	(0.0328)
Kobus leche	Light cover	MT	1	0.028	0.0308	-0.0004	0.0118	0.0212	-0.0036	-0.0475
		MC	1	0.0333	0.02	0.0157	0.0367	0.0254	0.0246	-0.0432
Kobus megaceros	Heavy cover	MT	6	0.0001	0.0009	-0.0047	-0.0014	0.0037	-0.0011	-0.1396
				(0.0245)	(0.0113)	(0.0054)	(0.0123)	(0.0086)	(0.0049)	(0.0615)

		MC	6	0.0018	-0.0044	-0.0012	0.0083	0.0014	0.0067	-0.1411
				(0.0154)	(0.0116)	(0.0122)	(0.0116)	(0.01)	(0.0072)	(0.0267)
Redunca arundinum	Light cover	MT	5	0.0255	0.0118	0.0026	0.0339	0.018	0.0074	-0.1205
				(0.0058)	(0.0083)	(0.0188)	(0.0079)	(0.0119)	(0.0182)	(0.0573)
		MC	5	0.0292	0.0102	0.0162	0.0449	0.0241	0.0276	-0.0997
				(0.0059)	(0.0093)	(0.0117)	(0.0102)	(0.0099)	(0.01)	(0.039)
Redunca fulvorufula	Light cover	MT	7	0.0067	0.0089	-0.0091	-0.0044	0.0076	-0.009	-0.1218
				(0.012)	(0.0057)	(0.0071)	(0.0077)	(0.0075)	(0.0085)	(0.0557)
		MC	7	0.0024	0.0013	-0.0086	0.0116	0.0101	0.001	-0.1072
				(0.0104)	(0.0087)	(0.0077)	(0.0142)	(0.0081)	(0.0053)	(0.0348)
Redunca redunca	Light cover	MT	5	0.0037	0.0112	0.0011	0.0074	0.0131	0.0012	-0.1583
				(0.0103)	(0.0116)	(0.0158)	(0.0085)	(0.0113)	(0.0118)	(0.0467)
		MC	5	0.0147	0.0021	0.0105	0.0317	0.0118	0.0178	-0.1196
				(0.012)	(0.0111)	(0.0152)	(0.0128)	(0.0097)	(0.0107)	(0.0246)

Table A5: Summary by species of medial-lateral distal epiphyseal variables based on analysis of complete metapodials.

Species	Habitat	Elem.	*N*	AVML	IVML	PVML	ADML	IDML	PDML	DEML	IIML
Antilocapridae											
Antilocaprinae											
Antilocaprini											
Antilocapra americana	Plains	MT	11	0.0181	0.0266	0.0135	0.0034	0.0078	0.0032	-0.0094	0.027
				(0.0137)	(0.0126)	(0.0163)	(0.0105)	(0.0084)	(0.0064)	(0.0087)	(0.0343)
		MC	6	0.0305	0.0282	0.0191	-0.0026	0.0035	0.0069	-0.0081	0.0458
				(0.0142)	(0.0121)	(0.015)	(0.0083)	(0.008)	(0.0137)	(0.0075)	(0.0353)
Bovidae											
Aepycerotinae											
Aepycerotini											
Aepyceros melampus	Light cover	MT	11	-0.0435	-0.0306	-0.0272	-0.0419	-0.0336	-0.0415	-0.0324	-0.0401
				(0.0295)	(0.0218)	(0.0245)	(0.0215)	(0.0175)	(0.0182)	(0.0154)	(0.0621)
		MC	11	-0.0149	-0.0152	-0.0187	-0.0347	-0.0321	-0.0305	-0.0271	0.0059
				(0.0109)	(0.0173)	(0.0134)	(0.0129)	(0.0147)	(0.0158)	(0.0124)	(0.0567)
Alcelaphinae											
Alcelaphini											
Alcelaphus buselaphus	Plains	MT	9	-0.004	0.0122	0.0012	0.0047	-0.0027	-0.0083	-0.0098	0.0296
				(0.0142)	(0.011)	(0.0128)	(0.0122)	(0.0092)	(0.0085)	(0.0096)	(0.0496)
		MC	9	0.0051	0.0229	0.003	0.0085	-0.0006	-0.0131	-0.0139	0.0543
				(0.015)	(0.0178)	(0.0118)	(0.0147)	(0.0083)	(0.0159)	(0.0089)	(0.047)
Alcelaphus lichtensteini	Plains	MT	1	-0.0177	0.0149	-0.002	0.0036	-0.0057	-0.0151	0.0098	0.1018
		MC	1	0.0044	0.0197	-0.0074	0.0019	-0.004	-0.009	0.0095	0.0869

Beatragus hunteri	Plains	MT	3	-0.007	0.013	-0.0048	0.0032	-0.0043	-0.0194	-0.0159	0.0024
				(0.0319)	(0.0085)	(0.0035)	(0.012)	(0.0038)	(0.0101)	(0.0161)	(0.0329)
		MC	3	-0.0119	0.0025	-0.0197	0.0248	-0.0014	-0.0206	-0.0102	0.0244
				(0.0088)	(0.009)	(0.0021)	(0.0168)	(0.0034)	(0.016)	(0.0254)	(0.05)
Connochaetes gnou	Plains	MT	4	0.0134	0.025	-0.0006	0.0209	0.0183	-0.0015	0.0056	0.0381
				(0.0252)	(0.0155)	(0.0154)	(0.0102)	(0.0056)	(0.0018)	(0.0091)	(0.08)
		MC	4	0.0439	0.0519	0.0255	0.0411	0.0391	0.0159	0.0165	0.0474
				(0.0144)	(0.021)	(0.0189)	(0.012)	(0.0039)	(0.0079)	(0.014)	(0.0802)
Connochaetes taurinus	Plains	MT	6	0.005	0.0259	0.0166	0.0334	0.0177	0.0139	0.0144	0.0531
				(0.0181)	(0.0116)	(0.0064)	(0.0182)	(0.0088)	(0.0137)	(0.0088)	(0.0839)
		MC	6	0.013	0.0391	0.0262	0.0327	0.0291	0.0197	0.018	0.0729
				(0.017)	(0.0135)	(0.0136)	(0.0101)	(0.0052)	(0.0194)	(0.01)	(0.1103)
Damaliscus dorcas	Plains	MT	5	0.0094	0.0162	-0.0072	0.015	0.0104	0.0008	0.0045	0.0032
				(0.0222)	(0.0216)	(0.0092)	(0.0124)	(0.0056)	(0.0071)	(0.0141)	(0.013)
		MC	5	0.0066	0.0279	-0.0044	0.01	0.0073	-0.0093	-0.002	0.0098
				(0.0114)	(0.0101)	(0.0064)	(0.0162)	(0.006)	(0.0118)	(0.0208)	(0.0071)
Damaliscus lunatus	Plains	MT	7	0.0118	0.0316	0.0112	0.0265	0.0135	0.0109	0.0102	0.033
				(0.0179)	(0.0133)	(0.0151)	(0.0148)	(0.0115)	(0.0149)	(0.016)	(0.0426)
		MC	7	0.0067	0.0216	-0.0057	0.0176	0.0101	-0.0088	-0.0006	0.0248
				(0.0155)	(0.0172)	(0.0139)	(0.0104)	(0.0124)	(0.0207)	(0.019)	(0.0389)
Antilopinae											
Antilopini											
Antidorcas marsupialis	Plains	MT	5	-0.0095	-0.013	-0.0067	-0.0082	-0.017	-0.0158	-0.0144	-0.0104
				(0.0216)	(0.0094)	(0.0081)	(0.011)	(0.008)	(0.0069)	(0.011)	(0.0397)
		MC	5	-0.0107	-0.0244	-0.0255	-0.0228	-0.0366	-0.036	-0.0329	-0.0277
				(0.0187)	(0.0045)	(0.015)	(0.0141)	(0.0064)	(0.0148)	(0.0087)	(0.0559)
Antilope cervicapra	Plains	MT	3	-0.0292	0.0052	0.0094	-0.0001	0.0059	-0.0038	-0.0046	-0.0293
				(0.0064)	(0.0133)	(0.0115)	(0.0221)	(0.0124)	(0.0062)	(0.0111)	(0.0148)

		MC	3	-0.0298	-0.0091	-0.0053	-0.0105	-0.0133	-0.0262	-0.0249	-0.0172
				(0.0164)	(0.0033)	(0.01)	(0.0081)	(0.0088)	(0.0004)	(0.0195)	(0.0183)
Eudorcas rufifrons	Plains	MT	1	-0.0169	0.0051	-0.0001	0.028	0.0103	-0.0023	-0.0042	-0.0011
		MC	1	-0.0273	0.004	0.0035	0.0273	0.001	-0.0064	-0.0167	0.0163
Eudorcas thomsoni	Plains	MT	6	-0.019	-0.0147	-0.003	0.0099	0.0017	-0.0052	0	0.0051
				(0.0228)	(0.007)	(0.0132)	(0.0129)	(0.0046)	(0.0104)	(0.013)	(0.0238)
		MC	6	-0.0033	-0.0151	-0.0069	0.0064	-0.0108	-0.0142	-0.0124	-0.0683
				(0.0144)	(0.0115)	(0.0169)	(0.0148)	(0.0027)	(0.0049)	(0.0066)	(0.0622)
Gazella gazella	Plains	MT	1	-0.0023	-0.0064	-0.0139	0.0886	0.0081	0.0071	0.0019	-0.0331
		MC	1	-0.0076	-0.0143	-0.0245	-0.0006	-0.0145	-0.0308	-0.0225	-0.0427
Litocranius walleri	Light cover	MT	5	-0.0688	-0.042	-0.0343	-0.0402	-0.0271	-0.0439	-0.0438	-0.0197
				(0.0138)	(0.0166)	(0.0124)	(0.0116)	(0.0097)	(0.004)	(0.0045)	(0.0482)
		MC	5	-0.0429	-0.0683	-0.0676	-0.06	-0.0629	-0.0744	-0.0782	-0.1081
				(0.0128)	(0.0139)	(0.0095)	(0.012)	(0.0102)	(0.017)	(0.01)	(0.0583)
Nanger granti	Plains	MT	9	-0.0157	-0.0121	-0.0058	-0.0053	-0.0131	-0.0203	-0.0207	-0.0097
				(0.0269)	(0.0125)	(0.0113)	(0.0177)	(0.0102)	(0.0099)	(0.0092)	(0.0452)
		MC	9	-0.014	-0.0249	-0.0156	-0.0181	-0.0311	-0.0381	-0.0435	-0.0387
				(0.0242)	(0.0112)	(0.0133)	(0.018)	(0.0114)	(0.0091)	(0.0145)	(0.0455)
Nanger soemmerringi	Plains	MT	2	-0.0151	-0.022	-0.0043	-0.0231	-0.0176	-0.026	-0.0232	0.0177
				(0)	(0.0026)	(0.008)	(0.0259)	(0.0014)	(0.0033)	(0.0055)	(0.0321)
		MC	2	-0.0252	-0.037	-0.0401	-0.0281	-0.0251	-0.0402	-0.0778	-0.0405
				(0.0077)	(0.0115)	(0.0154)	(0.003)	(0.0059)	(0.0012)	(0.0437)	(0.0218)
Neotragini											
Madoqua guentheri	Heavy cover	MT	3	-0.0074	0.013	-0.0071	-0.0024	0.0095	-0.0056	-0.0077	0.0261
				(0.0356)	(0.0121)	(0.0104)	(0.0084)	(0.0044)	(0.0073)	(0.0054)	(0.041)

		MC	3	-0.0017	0.0161	0.0208	0.0143	0.0171	0.0089	0.0001	0.0073
				(0.0334)	(0.0153)	(0.0038)	(0.0164)	(0.0056)	(0.0132)	(0.0046)	(0.0279)
Madoqua kirki	Heavy cover	MT	6	0.0286	0.0066	0.0049	0.0125	0.009	0.0073	0.0018	0.0421
				(0.0171)	(0.0223)	(0.0208)	(0.0099)	(0.0064)	(0.0074)	(0.0094)	(0.0551)
		MC	6	0.0267	0.0229	0.0134	0.0261	0.0258	0.0191	0.0187	0.0536
				(0.0124)	(0.0199)	(0.0112)	(0.0095)	(0.0105)	(0.0089)	(0.0091)	(0.0178)
Madoqua sp.	Heavy cover	MT	3	0.0061	0.0013	-0.0044	-0.0079	0.0035	-0.0068	-0.0079	0.0063
				(0.0173)	(0.0098)	(0.0136)	(0.0117)	(0.0067)	(0.004)	(0.0005)	(0.063)
		MC	3	0.0144	0.0124	0.0141	0.0163	0.0195	0.004	-0.0034	0.0536
				(0.0163)	(0.0131)	(0.0047)	(0.0103)	(0.0069)	(0.0043)	(0.0118)	(0.077)
Neotragus batesi	Forest	MT	1	0.0107	0.0215	0.0024	0.0124	0.0165	0.0134	0.0154	-0.1197
		MC	1	0.0241	0.0516	0.0456	0.0101	0.04	0.0397	0.028	-0.1254
Nesotragus moschatus	Forest	MT	1	0.0573	-0.0291	0.0195	-0.0121	0.0074	0.0168	0.0192	-0.0833
		MC	1	0.0137	0.0233	0.0186	0.0062	0.0315	0.0337	0.0363	-0.045
Oreotragus oreotragus	Mountain	MT	7	0.0141	0.0649	0.0566	0.0186	0.0333	0.0379	0.0258	0.1417
				(0.0127)	(0.0054)	(0.0065)	(0.016)	(0.0092)	(0.0062)	(0.0114)	(0.0276)
		MC	7	0.0627	0.0842	0.066	0.0524	0.0553	0.0668	0.046	0.1765
				(0.0119)	(0.0175)	(0.0137)	(0.0107)	(0.0092)	(0.0116)	(0.0087)	(0.0654)
Ourebia ourebi	Light cover	MT	7	0.0173	-0.0026	-0.0126	0.02	0.0028	-0.0058	-0.0049	-0.0428
				(0.0247)	(0.0113)	(0.0146)	(0.015)	(0.0112)	(0.0131)	(0.0138)	(0.0321)
		MC	7	-0.0124	-0.0112	-0.0046	0.0156	-0.0106	-0.0204	-0.0192	-0.0322
				(0.0222)	(0.0177)	(0.0156)	(0.0198)	(0.0127)	(0.0154)	(0.0164)	(0.0262)
Raphicerus campestris	Light cover	MT	5	0.0141	0.0086	0.0034	0.0212	0.0163	0.0206	-0.0242	0.0109
				(0.0211)	(0.01)	(0.0118)	(0.0154)	(0.0087)	(0.0089)	(0.1034)	(0.0372)

		MC	5	0.0063	0.0264	0.0281	0.0327	0.0189	0.0056	0.0019	0.0026
				(0.0342)	(0.0223)	(0.0269)	(0.0216)	(0.0167)	(0.0188)	(0.0249)	(0.085)
Raphicerus sharpei	Light cover	MT	1	0.0612	0.0176	0.0202	0.0319	0.017	0.0221	0.0153	0.0754
		MC	1	0.037	0.0347	0.0245	0.0363	0.0275	0.0285	0.0175	0.0588
Saigini											
Saiga tatarica	Plains	MT	3	0.0314	0.0365	0.0247	0.0304	0.0222	0.0155	0.0113	0.0772
				(0.0213)	(0.0124)	(0.0068)	(0.0089)	(0.0042)	(0.0033)	(0.0008)	(0.0341)
		MC	3	0.0359	0.0256	0.0238	0.0382	0.0109	0.0073	0.0053	0.0537
				(0.009)	(0.0188)	(0.0119)	(0.0117)	(0.0087)	(0.0106)	(0.0074)	(0.015)
Bovinae											
Boselaphini											
Boselaphus tragocamelus	Heavy cover	MT	5	-0.0362	-0.0449	-0.0559	-0.0472	-0.0367	-0.0305	-0.032	-0.0911
				(0.019)	(0.0106)	(0.02)	(0.0205)	(0.0029)	(0.0111)	(0.0207)	(0.0793)
		MC	6	-0.0437	-0.0357	-0.0426	-0.0174	-0.0214	-0.0209	-0.0125	-0.0761
				(0.0321)	(0.0184)	(0.0254)	(0.0208)	(0.0083)	(0.0093)	(0.0164)	(0.0977)
Tetracerus quadricornis	Heavy cover	MT	4	0.0336	0.0062	-0.0049	-0.0069	-0.0166	-0.0193	0.0082	0.0923
				(0.0249)	(0.0061)	(0.0127)	(0.0229)	(0.0152)	(0.0218)	(0.018)	(0.1164)
		MC	3	-0.0213	-0.0257	-0.012	-0.018	-0.0315	-0.0367	0.0096	-0.0969
				(0.0161)	(0.007)	(0.0051)	(0.0117)	(0.0093)	(0.0081)	(0.0051)	(0.0437)
Bovini											
Anoa depressicornis	Forest	MT	6	0.0074	0.0411	0.0267	0.0102	0.0387	0.0375	0.0304	0.0672
				(0.0201)	(0.0143)	(0.0085)	(0.0218)	(0.0062)	(0.0066)	(0.006)	(0.0523)
		MC	6	0.0078	0.0395	0.0296	0.0275	0.0517	0.0525	0.0489	0.0957
				(0.0143)	(0.0067)	(0.0112)	(0.01)	(0.0083)	(0.0125)	(0.0099)	(0.0446)
Anoa mindorensis	Forest	MT	2	0.0003	0.0556	0.0395	0.0557	0.0518	0.054	0.0447	0.0659
				(0.0189)	(0.0051)	(0.0085)	(0.0061)	(0.0067)	(0.0015)	(0.0008)	(0.0474)

		MC	2	0.0276	0.0392	0.039	0.066	0.0461	0.051	0.0494	0.0773
				(0.0109)	(0.0041)	(0.01)	(0.0179)	(0.008)	(0.0072)	(0.0054)	(0.1076)
Bison bison athabaskae	Light cover	MT	5	0.0445	0.0066	0.0118	0.0094	0.023	0.0133	0.0049	0.1078
				(0.011)	(0.0564)	(0.0132)	(0.0095)	(0.0068)	(0.0062)	(0.0082)	(0.0307)
		MC	5	0.0139	0.0233	0.0108	0.0005	0.0129	0.0161	0.0072	0.0229
				(0.0126)	(0.0108)	(0.0143)	(0.0089)	(0.006)	(0.0076)	(0.0082)	(0.0518)
Bison bison bison	Plains	MT	6	0.0438	0.0456	0.0311	0.019	0.032	0.021	0.0119	0.0674
				(0.0337)	(0.0227)	(0.0214)	(0.017)	(0.0137)	(0.0156)	(0.0138)	(0.0692)
		MC	5	0.0042	0.0256	0.0268	0.0291	0.0216	0.0258	0.009	-0.0195
				(0.0265)	(0.0186)	(0.0184)	(0.0202)	(0.0081)	(0.0126)	(0.0179)	(0.0824)
Bos gaurus	Heavy cover	MT	5	0.0162	-0.0082	-0.0025	-0.0147	0.0004	-0.0042	-0.0072	0.0182
				(0.0189)	(0.0157)	(0.0106)	(0.0109)	(0.0045)	(0.0084)	(0.0048)	(0.0375)
		MC	5	-0.002	-0.0118	-0.0057	-0.0029	0.0027	0.0004	0.0027	-0.0322
				(0.011)	(0.0048)	(0.0044)	(0.0089)	(0.0082)	(0.0084)	(0.0074)	(0.0526)
Bos grunniens	Mountain	MT	4	0.0534	0.0487	0.0268	0.0356	0.042	0.0352	0.0233	0.0213
				(0.0276)	(0.0194)	(0.0148)	(0.0128)	(0.0135)	(0.0077)	(0.0068)	(0.0311)
		MC	4	0.0356	0.0517	0.037	0.0241	0.052	0.0531	0.0412	-0.0101
				(0.0288)	(0.0323)	(0.0201)	(0.0083)	(0.0138)	(0.0102)	(0.0063)	(0.0516)
Bos sauveli	Heavy cover	MT	2	0.0159	0.0336	0.0146	-0.0051	0.0102	-0.0014	-0.0055	0.0239
				(0.0117)	(0.0041)	(0.0022)	(0.006)	(0.0044)	(0.0199)	(0.0103)	(0.0217)
		MC	2	-0.0138	0.0191	0.0113	-0.011	0.0059	0.0111	0.0021	0.0004
				(0.0472)	(0.0276)	(0.017)	(0.0205)	(0.0262)	(0.0286)	(0.0295)	(0.0074)
Bubalis bubalis	Heavy cover	MT	1	0.0184	0.057	0.0706	0.0899	0.056	0.0568	0.0521	0.1253
		MC	1	0.0228	0.0575	0.0663	0.0472	0.0679	0.0776	0.058	0.1517
Syncerus caffer caffer	Light cover	MT	3	0.021	0.0137	0.0116	0.0309	0.0207	0.0309	0.0202	0.0293
				(0.0204)	(0.016)	(0.0081)	(0.0178)	(0.0087)	(0.0041)	(0.0083)	(0.0183)

		MC	3	0.002	0.0079	0.0192	0.0436	0.0263	0.0427	0.0341	0.0437
				(0.0365)	(0.0246)	(0.009)	(0.0058)	(0.007)	(0.0028)	(0.0067)	(0.0607)
Syncerus caffer nanus	Heavy cover	MT	3	0.0328	0.0437	0.0299	0.0302	0.0381	0.0395	0.0237	-0.0136
				(0.0256)	(0.0087)	(0.002)	(0.0128)	(0.0067)	(0.0072)	(0.0112)	(0.0501)
		MC	3	0.0184	0.0316	0.0241	0.0323	0.0392	0.0464	0.0358	0.0584
				(0.0318)	(0.0198)	(0.0151)	(0.0203)	(0.0086)	(0.0154)	(0.0148)	(0.0363)
Tragelaphini											
Tragelaphus angasi	Heavy cover	MT	1	-0.1058	-0.1045	-0.1002	-0.0896	-0.0717	-0.0363	-0.0393	-0.1609
		MC	1	-0.0776	-0.0884	-0.0729	-0.0467	-0.048	-0.0503	-0.0415	-0.2546
Tragelaphus derbianus	Light cover	MT	1	-0.0025	-0.0192	-0.0281	-0.0088	-0.0276	-0.0206	-0.0312	-0.0755
		MC	1	-0.0181	-0.0337	-0.0245	-0.0156	-0.029	-0.0278	-0.0088	0.0024
Tragelaphus eurycerus	Forest	MT	9	-0.0307	-0.0504	-0.0298	-0.0333	-0.0459	-0.0334	-0.0274	-0.0207
				(0.0178)	(0.0183)	(0.0195)	(0.0084)	(0.0087)	(0.0049)	(0.0095)	(0.0581)
		MC	9	-0.0238	-0.0369	-0.0166	-0.0374	-0.0287	-0.0185	-0.0069	-0.0061
				(0.0176)	(0.0241)	(0.0107)	(0.0139)	(0.0089)	(0.0096)	(0.0069)	(0.0506)
Tragelaphus imberbis	Heavy cover	MT	5	-0.0944	-0.1067	-0.0763	-0.065	-0.0786	-0.0567	-0.0491	-0.1491
				(0.0234)	(0.0257)	(0.017)	(0.0295)	(0.0161)	(0.0127)	(0.0088)	(0.0478)
		MC	5	-0.087	-0.0836	-0.0614	-0.0729	-0.0744	-0.0671	-0.0541	-0.2025
				(0.0248)	(0.018)	(0.0147)	(0.0182)	(0.0098)	(0.0167)	(0.0094)	(0.0684)
Tragelaphus oryx	Light cover	MT	6	-0.0326	-0.0171	-0.0185	-0.0105	-0.0114	-0.0092	-0.0163	-0.0946
				(0.0178)	(0.0148)	(0.0134)	(0.0217)	(0.0094)	(0.0082)	(0.01)	(0.0595)
		MC	6	-0.0429	-0.0246	-0.0279	-0.0084	-0.0147	-0.0149	-0.0229	-0.0689
				(0.0245)	(0.0135)	(0.0122)	(0.0441)	(0.0056)	(0.0043)	(0.0057)	(0.0448)

Tragelaphus scriptus	Forest	MT	14	-0.0379	-0.0479	-0.0338	-0.0583	-0.0504	-0.0389	-0.0336	-0.0845
				(0.0307)	(0.0264)	(0.0196)	(0.0234)	(0.017)	(0.0137)	(0.0191)	(0.0749)
		MC	15	-0.0412	-0.0572	-0.0446	-0.0635	-0.0471	-0.0358	-0.0292	-0.0833
				(0.0318)	(0.0275)	(0.0216)	(0.02)	(0.0142)	(0.0135)	(0.0169)	(0.0757)
Tragelaphus spekei	Heavy cover	MT	6	-0.1038	-0.0559	-0.0446	-0.0651	-0.032	-0.0234	-0.0074	-0.1624
				(0.0301)	(0.0208)	(0.0196)	(0.0212)	(0.0141)	(0.0158)	(0.0115)	(0.0805)
		MC	6	-0.0884	-0.0705	-0.045	-0.0711	-0.0317	-0.0309	-0.0178	-0.1875
				(0.0321)	(0.0256)	(0.0147)	(0.0142)	(0.0136)	(0.0145)	(0.0119)	(0.066)
Tragelaphus strepsiceros	Heavy cover	MT	7	-0.0569	-0.0817	-0.0677	-0.057	-0.0639	-0.0552	-0.0492	-0.1031
				(0.0192)	(0.0218)	(0.0186)	(0.0192)	(0.0107)	(0.0115)	(0.0146)	(0.0471)
		MC	6	-0.0549	-0.0804	-0.07	-0.0816	-0.065	-0.0561	-0.0529	-0.0673
				(0.0171)	(0.0169)	(0.007)	(0.0173)	(0.0156)	(0.0151)	(0.0184)	(0.05)
Caprinae											
Caprini											
Ammotragus lervia	Mountain	MT	4	0.0781	0.0281	0.0227	0.0578	0.0406	0.0462	0.048	0.0671
				(0.0259)	(0.0216)	(0.0446)	(0.0526)	(0.0264)	(0.029)	(0.022)	(0.0539)
		MC	4	0.0881	0.0396	0.0348	0.061	0.045	0.0329	0.034	0.0927
				(0.0206)	(0.0194)	(0.0127)	(0.0311)	(0.0186)	(0.0143)	(0.0153)	(0.0742)
Ovis ammon	Mountain	MT	5	0.0205	0.001	-0.0137	0.0222	0.0104	0.0115	0.0109	0.0342
				(0.0108)	(0.0136)	(0.0141)	(0.0208)	(0.007)	(0.0096)	(0.0079)	(0.046)
		MC	5	0.0256	-0.0028	0.003	0.0179	0.0062	-0.0023	-0.0117	0.0818
				(0.008)	(0.0117)	(0.0141)	(0.0178)	(0.0031)	(0.0067)	(0.0028)	(0.0362)
Pantholopini											
Pantholops hodgsoni	Plains	MT	1	0.0154	0.0191	-0.0122	-0.0089	0.0141	-0.027	-0.0228	-0.0188
		MC	1	0.0379	0.0167	-0.0096	-0.0096	0.0025	-0.0171	-0.0183	0.0379
Rupicaprini											

Budorcas taxicolor	Mountain	MT	1	0.0631	0.0432	0.0493	0.0443	0.0474	0.0571	0.042	-0.033
		MC	1	0.0772	0.0513	0.0548	0.0769	0.0527	0.0456	0.0289	0.0292
Myotragus balearicus	Mountain	MT	1	0.0861	0.0335	-0.0433	0.0978	0.0411	0.0058	0.0155	0.0664
		MC	1	0.1201	0.0654	-0.0036	0.1054	0.0455	0.0274	0.0317	0.2196
Naemorhedus crispus	Mountain	MT	1	0.1165	0.1149	0.0986	0.078	0.0842	0.0914	0.0757	0.2205
		MC	1	0.0952	0.1031	0.0934	0.0657	0.0748	0.0865	0.0649	0.2343
Naemorhedus goral	Mountain	MT	7	0.0584	0.0766	0.0737	0.0666	0.0674	0.0644	0.0572	0.1163
				(0.0306)	(0.0085)	(0.0077)	(0.0149)	(0.0122)	(0.0136)	(0.009)	(0.0358)
		MC	7	0.0718	0.0687	0.0677	0.0653	0.0656	0.0645	0.0471	0.1578
				(0.0283)	(0.02)	(0.0148)	(0.01)	(0.0082)	(0.0074)	(0.0061)	(0.0833)
Naemorhedus sumatraensis	Mountain	MT	5	0.045	0.0338	0.0544	0.009	0.0359	0.0458	0.0337	0.0521
				(0.0245)	(0.0134)	(0.0066)	(0.0106)	(0.0064)	(0.0127)	(0.0127)	(0.0237)
		MC	5	0.0508	0.0244	0.0307	0.0219	0.0271	0.0368	0.0188	0.0832
				(0.0331)	(0.0252)	(0.0214)	(0.0166)	(0.0149)	(0.0087)	(0.0088)	(0.0111)
Naemorhedus swinhoei	Mountain	MT	1	0.0268	0.0438	0.059	0.0575	0.0755	0.0758	0.0721	0.0603
		MC	1	0.069	0.0479	0.07	0.0758	0.0735	0.0869	0.0692	0.0394
Oreamnos americanus	Mountain	MT	3	0.133	0.076	0.0575	0.0744	0.0817	0.0913	0.0825	0.1516
				(0.0155)	(0.0078)	(0.0053)	(0.0023)	(0.005)	(0.0094)	(0.0014)	(0.0113)
		MC	3	0.1452	0.0996	0.0897	0.1022	0.0835	0.0823	0.0833	0.2425
				(0.0019)	(0.0066)	(0.0099)	(0.015)	(0.0023)	(0.0071)	(0.0045)	(0.0437)

Rupicapra rupicapra	Mountain	MT	1	0.0546	0.0594	0.0541	0.0429	0.0675	0.0648	0.0588	0.1228
		MC	1	0.068	0.0615	0.0624	0.0622	0.0638	0.0591	0.0494	0.1687
Cephalophinae											
Cephalophini											
Cephalophus dorsalis	Forest	MT	5	0.0005	-0.0232	-0.0158	-0.0193	-0.0086	0.0034	0.0153	-0.0456
				(0.0248)	(0.0127)	(0.019)	(0.0207)	(0.0072)	(0.0171)	(0.0082)	(0.0542)
		MC	5	-0.0168	-0.0045	-0.0085	-0.0044	0.0091	0.031	0.0397	-0.0038
				(0.0183)	(0.0121)	(0.0186)	(0.0241)	(0.0092)	(0.0151)	(0.0121)	(0.0634)
Cephalophus leucogaster	Forest	MT	5	-0.0471	-0.028	-0.0276	-0.0025	-0.0157	-0.005	-0.0022	0.0409
				(0.0316)	(0.008)	(0.0197)	(0.0145)	(0.0072)	(0.012)	(0.013)	(0.0547)
		MC	5	-0.0478	-0.0113	-0.0195	0.0025	0.0045	0.0168	0.018	0.0558
				(0.0159)	(0.0225)	(0.0115)	(0.0097)	(0.0101)	(0.0124)	(0.0117)	(0.08)
Cephalophus sylvicultor	Forest	MT	7	0.0223	-0.0294	0.0021	0.0057	-0.0039	0.0089	0.0147	-0.0446
				(0.0193)	(0.0225)	(0.0121)	(0.0102)	(0.0077)	(0.0086)	(0.0051)	(0.061)
		MC	7	0.0083	-0.0318	0.0184	-0.0022	0.0016	0.0238	0.0313	0.0205
				(0.0239)	(0.0178)	(0.018)	(0.0089)	(0.0119)	(0.0128)	(0.0095)	(0.0386)
Cephalophus weynsi	Forest	MT	1	-0.0135	-0.0146	-0.0198	0.0107	0.0013	0.0071	0.0049	-0.1369
		MC	1	-0.0086	-0.0175	-0.0446	0.0119	0	0.0014	0.0065	-0.0511
Philantomba monticola	Forest	MT	1	-0.0762	-0.0882	-0.0136	-0.0428	-0.0525	-0.0247	-0.0114	0.0204
		MC	1	-0.0307	-0.0237	-0.0054	-0.0148	-0.0252	-0.0078	0.0008	0.1446
Sylvicapra grimmia	Light cover	MT	7	-0.0151	-0.0495	-0.0503	-0.0407	-0.0314	-0.0146	-0.022	-0.1215
				(0.016)	(0.02)	(0.0202)	(0.0125)	(0.0081)	(0.0188)	(0.0215)	(0.0517)

		MC	9	-0.044	-0.0371	-0.0486	-0.0279	-0.0141	-0.0035	-0.0085	-0.102
				(0.0309)	(0.0194)	(0.0149)	(0.0175)	(0.0129)	(0.0181)	(0.0232)	(0.0551)
Hippotraginae											
Hippotragini											
Addax nasomaculatus	Plains	MT	4	0.0603	0.0595	0.0368	0.0408	0.0594	0.0469	0.0388	0.0866
				(0.0039)	(0.0047)	(0.0082)	(0.0116)	(0.0015)	(0.0036)	(0.0033)	(0.0144)
		MC	4	0.0769	0.0735	0.0501	0.0574	0.058	0.0492	0.0312	0.0822
				(0.0124)	(0.0097)	(0.0075)	(0.01)	(0.0045)	(0.0039)	(0.0058)	(0.0362)
Hippotragus equinus	Light cover	MT	5	0.0018	0.0001	-0.005	0.0039	0.0027	0.006	0.0013	0.0187
				(0.0247)	(0.0213)	(0.0083)	(0.0081)	(0.0122)	(0.0038)	(0.01)	(0.0516)
		MC	5	0.0026	0.0029	-0.0065	0.0105	-0.0012	0.0001	-0.0026	-0.0155
				(0.0219)	(0.0299)	(0.0197)	(0.0228)	(0.0149)	(0.0118)	(0.0168)	(0.0777)
Hippotragus niger	Light cover	MT	6	0.0386	0.0107	0.0059	0.0133	0.0099	0.0073	0.0206	0.0052
				(0.0146)	(0.0179)	(0.0171)	(0.0157)	(0.012)	(0.0123)	(0.0215)	(0.0456)
		MC	6	0.0208	0.0113	0.0087	-0.0155	0.0104	0.0066	0.0221	0.0037
				(0.0131)	(0.0131)	(0.0113)	(0.0636)	(0.0075)	(0.0106)	(0.0221)	(0.05)
Oryx beisa	Plains	MT	2	-0.0092	-0.0026	0.0035	0.0109	0.0212	0.0144	0.0147	0.0265
				(0.003)	(0.0171)	(0.0121)	(0.021)	(0.0079)	(0.014)	(0.0224)	(0.0941)
		MC	2	0.0154	0.0088	-0.0052	-0.0012	0.0175	0.0096	0.0032	0.0811
				(0.0349)	(0.0029)	(0.0064)	(0.0064)	(0.0039)	(0.0134)	(0.0156)	(0.0457)
Oryx dammah	Plains	MT	2	0.0049	0.005	0.004	0.0026	0.0184	0.0085	0.013	0.0237
				(0.0294)	(0.0043)	(0.0069)	(0.004)	(0.0085)	(0.0019)	(0.0024)	(0.0523)
		MC	2	0.0284	-0.0024	-0.0014	0.0114	0.0135	0.0139	0.013	-0.015
				(0.0034)	(0.0115)	(0.0013)	(0.013)	(0.0096)	(0.0013)	(0.0066)	(0.0311)
Oryx gazella	Plains	MT	2	0.0022	0.0188	0.0006	0.0201	0.0157	0.0096	0.0086	0.0514
				(0.0326)	(0.0033)	(0.0077)	(0.0063)	(0.0055)	(0.014)	(0.0121)	(0.0165)
		MC	2	0.0158	0.0273	0.0045	0.0201	0.0229	0.0102	0.0105	0.0645
				(0.0146)	(0.0101)	(0.0098)	(0.014)	(0.0108)	(0.0012)	(0.0015)	(0.0153)
Oryx leucoryx	Plains	MT	1	0.073	0.0465	0.0192	0.026	0.0409	0.0273	0.0177	0.0608

		MC	1	0.0598	0.0655	0.0242	0.0374	0.0425	0.0467	0.0227	0.1667
Reduncinae											
Reduncini											
Kobus ellipsiprymnus	Heavy cover	MT	7	0.0139	0.0161	0.0287	0.0229	0.0071	0.016	0.0166	0.0287
				(0.0295)	(0.018)	(0.0097)	(0.0113)	(0.012)	(0.009)	(0.0069)	(0.0241)
		MC	8	0.0061	0.0064	0.0154	0.0139	0.003	0.0075	0.0026	0.0273
				(0.0387)	(0.0152)	(0.009)	(0.0127)	(0.0101)	(0.0137)	(0.0144)	(0.0596)
Kobus kob	Light cover	MT	9	-0.0047	0.0078	0.0227	0.0184	0.0116	0.0087	0.0167	-0.0305
				(0.0194)	(0.013)	(0.0126)	(0.0147)	(0.0083)	(0.0069)	(0.0119)	(0.0615)
		MC	9	-0.0049	0.0005	0.0177	0.0033	0.0051	0.0074	0.0164	-0.046
				(0.0152)	(0.0163)	(0.012)	(0.0178)	(0.0094)	(0.0109)	(0.0144)	(0.0655)
Kobus leche	Light cover	MT	1	-0.0192	0.0098	0.0105	0.0038	0.0133	0.0137	0.0083	-0.0166
		MC	1	-0.0303	-0.0109	-0.0064	-0.056	-0.0093	-0.0004	-0.0216	-0.1009
Kobus megaceros	Heavy cover	MT	6	0.0008	0.0097	0.03	-0.0146	0.0045	0.0069	0.0179	0.0064
				(0.0255)	(0.023)	(0.0148)	(0.0599)	(0.0113)	(0.0105)	(0.0072)	(0.0627)
		MC	6	0.0116	0.0021	0.0194	-0.0049	-0.0027	-0.0043	0.0122	-0.0446
				(0.0169)	(0.0147)	(0.0074)	(0.0135)	(0.009)	(0.0103)	(0.0062)	(0.0639)
Redunca arundinum	Light cover	MT	5	-0.0421	-0.0308	-0.007	-0.03	-0.0354	-0.0302	-0.0219	-0.0777
				(0.0106)	(0.0127)	(0.0256)	(0.0162)	(0.0109)	(0.0085)	(0.0117)	(0.0459)
		MC	5	-0.0325	-0.0318	-0.0107	-0.0401	-0.0434	-0.0362	-0.0252	-0.1122
				(0.0229)	(0.0084)	(0.0192)	(0.0166)	(0.0086)	(0.0078)	(0.0146)	(0.0515)
Redunca fulvorufula	Light cover	MT	7	0.0077	0.0232	0.0157	0.0071	-0.0055	-0.013	-0.0014	-0.0095
				(0.026)	(0.0109)	(0.0113)	(0.0165)	(0.0117)	(0.0088)	(0.015)	(0.0361)
		MC	7	0.0025	0.0043	0.0081	-0.0022	-0.01	-0.0096	-0.001	-0.0102
				(0.0089)	(0.0135)	(0.0122)	(0.0138)	(0.0095)	(0.0128)	(0.012)	(0.0376)

Redunca redunca	Light cover	MT	5	-0.0233	-0.0169	-0.0031	-0.0137	-0.033	-0.0219	-0.0132	-0.068
				(0.0286)	(0.0222)	(0.0129)	(0.011)	(0.0114)	(0.011)	(0.0098)	(0.0446)
		MC	5	-0.0162	-0.0261	-0.0167	-0.0223	-0.0417	-0.0297	-0.0183	-0.0808
				(0.0225)	(0.0155)	(0.0108)	(0.0061)	(0.0085)	(0.0154)	(0.018)	(0.0569)

APPENDIX B: FOSSIL BOVID SAMPLE.

Table B1: Estimated body masses and probable habitat classifications for fossil bovid specimens.

Specimen	Site	Species	Elem.	Estimated body mass (complete analysis)	Estimated body mass (distal analysis)	Most likely habitat (complete analysis)	Second most likely habitat (complete analysis)	Most likely habitat (distal analysis)	Second most likely habitat (distal analysis)
IPS BA 20617	Ballestar		MC	68.6 [m/d 1.68]	64.8 [m/d 1.73]	Heavy cover [0.564]	Light cover [0.436]	Light cover [0.967]	Forest [0.022]
IPS 2548	Can Llobateres		MC	28.7 [m/d 1.68]	25.3 [m/d 1.74]	Heavy cover [0.816]	Light cover [0.181]	Forest [0.516]	Mountain [0.466]
IPS CLL 20603	Can Llobateres		MC	111.1 [m/d 1.68]	102.2 [m/d 1.73]	Light cover [0.717]	Heavy cover [0.282]	Heavy cover [0.739]	Forest [0.142]
YPM VP20693	Pikermi		MT	26.2 [m/d 1.48]	22.7 [m/d 1.49]	Heavy cover [0.841]	Forest [0.117]	Forest [0.999]	Heavy cover [0.001]
YPM VP20692	Pikermi		MT		161.4 [m/d 1.49]			Heavy cover [0.638]	Forest [0.227]
IPS 1237	Torrent de Fibulines		MC	195.2 [m/d 1.68]	196.8 [m/d 1.74]	Heavy cover [0.988]	Light cover [0.006]	Heavy cover [0.899]	Light cover [0.06]
GSP46146	Y0076		MC		31.6 [m/d 1.74]			Forest [1]	Heavy cover [0]
GSP32407	Y0076		MT		31.3 [m/d 1.49]			Forest [0.919]	Light cover [0.057]
GSP 47808	Y0311	cf. Tragoceridus pilgrimi	MC		62.3 [m/d 1.73]			Forest [0.67]	Mountain [0.296]
GSP10569	Y0311	cf. Tragoceridus pilgrimi	MC		50.6 [m/d 1.73]			Forest [0.492]	Heavy cover [0.486]

GSP12203	Y0311	cf. Tragoceridus pilgrimi	MC		64.4 [m/d 1.73]			Forest [0.793]	Light cover [0.207]
GSP 47806	Y0311	cf. Tragoceridus pilgrimi	MC		57.2 [m/d 1.73]			Heavy cover [0.58]	Light cover [0.382]
GSP 47809	Y0311	cf. Selenoportax sp.	MC		142.1 [m/d 1.74]			Heavy cover [0.87]	Light cover [0.103]
GSP 47807	Y0311	cf. Selenoportax sp.	MC		105.7 [m/d 1.73]			Heavy cover [0.644]	Light cover [0.323]
GSP 46729	Y0311	cf. Tragoceridus pilgrimi	MC	57.8 [m/d 1.68]	60.5 [m/d 1.73]	Heavy cover [0.872]	Light cover [0.12]	Heavy cover [0.828]	Light cover [0.169]
GSP 47811	Y0311	cf. Tragoceridus pilgrimi	MT		64.4 [m/d 1.49]			Light cover [0.87]	Heavy cover [0.125]
GSP 46737	Y0311	cf. Tragoceridus pilgrimi	MT	52.6 [m/d 1.48]	49.8 [m/d 1.49]	Heavy cover [0.73]	Plains [0.251]	Light cover [0.758]	Heavy cover [0.196]
GSP6477	Y0311	cf. Tragoceridus pilgrimi	MC		57.6 [m/d 1.73]			Light cover [0.759]	Heavy cover [0.203]
GSP14101	Y0311	cf. Selenoportax sp.	MC		101.3 [m/d 1.73]			Light cover [0.791]	Heavy cover [0.188]
GSP26869	Y0311	cf. Tragoceridus pilgrimi	MT		54.7 [m/d 1.49]			Light cover [0.822]	Heavy cover [0.159]
GSP12154	Y0311	cf. Tragoceridus pilgrimi	MC		55.3 [m/d 1.73]			Light cover [0.958]	Mountain [0.02]
GSP 47810	Y0311	cf. Selenoportax sp.	MT		116.1 [m/d 1.49]			Mountain [0.309]	Light cover [0.271]

				16.1	Heavy cover	Forest
GSP45529	Y0496	MT		[m/d 1.49]	[0.983]	[0.017]
			43.4	40.5	Light cover	Forest
GSP45541	Y0496	MC	[m/d 1.68]	[m/d 1.73]	[0.867]	[0.067]
			33.2	33	Light cover	Mountain
GSP45540	Y0496	MT	[m/d 1.48]	[m/d 1.49]	[0.892]	[0.054]
			42.7	37.4	Mountain	Forest
GSP45524	Y0496	MC	[m/d 1.68]	[m/d 1.73]	[0.909]	[0.078]

[#] denotes posterior probability of habitat classification; [m/d #] denotes multiplied or divided by standard error for body mass estimates given in kilograms.

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Vita

Robert Smith Scott was born in Missoula, Missoula County, Montana on August 20, 1972. He is the son of Robert Benson Scott and Glenna Smith Scott. He graduated from Hamilton High School in Ravalli County, Montana in 1990. He was awarded a B.A. in Anthropology and Organismal Biology *with distinction* from Yale University in 1994 and a M.A. in Anthropology from The University of Texas at Austin in 1996. Scholarly publications include contributions to the book Geology and Paleontology of the Miocene Sinap, Formation, Turkey and to the to the journals *Geodiversitas*, *Journal of Human Evolution*, *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie*, *Senckenbergiana Lethaea*, and *Coloquios de Paleontología*. He has taught *Introduction to Physical Anthropology* at The University of Texas at Austin. He is married to Shannon Wehling Scott and their marriage was recorded in Williamson County, Texas in October, 1998. Robert and Shannon have one son, Robert Charles Scott, born in Austin, Travis County, Texas on December 15, 2002. Robert and his family are members of Saint David's Episcopal Church in Austin, Texas.

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